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FLORA COSTARICENSIS

- FAMILY #54 PODOSTEMACEAE
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- FAMILY #68 PORTULACACEAE
- FAMILY #69 BASELLACEAE
- FAMILY #70 CARYOPHYLLACEAE

WILLIAM BURGER, Editor

December 29, 1983

Publication 1350

Families of seed plants known or expected to occur in Costa Rica and adjacent areas, listed alphabetically and numbered according to the sequence of Engler's *Syllabus der Pflanzenfamilien*, edition 11, reworked by L. Diels (1936).

200	Acanthaceae	102	Erythroxylaceae	17	Palmae
136	Actinidiaceae	113	Euphorbiaceae	82	Papaveraceae
67	Aizoaceae	96	Fabaceae,	150	Passifloraceae
11	Alismataceae		see Leguminosae	195	Pedaliaceae
64	Amaranthaceae	50	Fagaceae	66	Phytolaccaceae
30	Amaryllidaceae	148	Flacourtiaceae	5	Pinaceae
117	Anacardiaceae	82	Fumariaceae,	41	Piperaceae
77	Anonaceae		see Papaveraceae	171	Pyrolaceae
184	Apocynaceae	45	Garryaceae	201	Plantaginaceae
119	Aquifoliaceae	183	Gentianaceae	176	Plumbaginaceae
19	Araceae	99	Geraniaceae	3	Podocarpaceae
166	Araliaceae	198	Gesneriaceae	54	Podostemonaceae
4	Aracariaceae	7	Gnetaceae	187	Polemoniaceae
59	Aristolochiaceae	15	Gramineae	111	Polygalaceae
185	Asclepiadaceae	142	Guttiferae	62	Polygonaceae
61	Balanophoraceae	29	Haemodoraceae	26	Pontederiaceae
127	Balsaminaceae	165	Halorrhagaceae	68	Portulacaceae
69	Basellaceae	93	Hamamelidaceae	9	Potamogetonaceae
48	Batidaceae	81	Hernandiaceae	175	Primulaceae
153	Begoniaceae	124	Hippocastanaceae	55	Proteaceae
74	Berberidaceae	121	Hippocrateaceae	158	Punicaceae
49	Betulaceae	101	Humiriaceae,	140	Quinnaceae
194	Bignoniaceae		see Linaceae	60b	Rafflesiaceae
145	Bixaceae	60a	Hydnoraceae	73	Ranunculaceae
133	Bombacaceae	13	Hydrocharitaceae	86	Resedaceae
189	Boraginaceae	188	Hydrophyllaceae	128	Rhamnaceae
24	Bromeliaceae	142	Hypericaceae,	160	Rhizophoraceae
91	Brunelliaceae		see Guttiferae	94	Rosaceae
38	Burmanniaceae	123	Icacinaceae	202	Rubiaceae
106	Burseraceae	33	Iridaceae	104	Rutaceae
12	Butomaceae	47	Juglandaceae	126	Sabiaceae
115	Buxaceae	27	Juncaceae	44	Salicaceae
154	Cactaceae	97	Krameriaceae	125	Sapindaceae
96	Caesalpinjiaceae,	191	Labiatae	177	Sapotaceae
	see Leguminosae	43	Lacistemaceae	90	Saxifragaceae
114	Callitrichaceae	80	Lauraceae	193	Scrophulariaceae
207	Campanulaceae	159	Lecythidaceae	105	Simarubaceae
36	Cannaceae	96	Leguminosae	192	Solanaceae
83	Capparidaceae	20	Lemnaceae	122	Staphyleaceae
203	Caprifoliaceae	199	Lentibulariaceae	134	Sterculiaceae
151	Caricaceae	28	Liliaceae	180	Styracaceae
138	Caryocaraceae	101	Linaceae	179	Symplocaceae
70	Caryophyllaceae	152	Loasaceae	2	Taxaceae
40	Casuarinaceae	182	Loganiaceae	141	Theaceae
120	Celastraceae	58	Loranthaceae	173	Theophrastaceae
72	Ceratophyllaceae	157	Lythraceae	155	Thymelaeaceae
63	Chenopodiaceae	76	Magnoliaceae	131	Tiliaceae
42	Chloranthaceae	108	Malpighiaceae	85	Tovariaceae
144	Cistaceae	132	Malvaceae	109	Trigoniaceae
169	Clethraceae	37	Marantaceae	14	Triuridaceae
146	Cochlospermaceae	139	Marcgraviaceae	100	Tropaeolaceae
161	Combretaceae	196	Martyniaceae	149	Turneraceae
25	Commelinaceae	21	Mayaceae	8	Typhaceae
208	Compositae	163	Melastomataceae	51	Ulmaceae
95	Connaraceae	107	Meliaceae	167	Umbelliferae
186	Convolvulaceae	75	Menispermaceae	53	Urticaceae
116	Coriariaceae	96	Mimosaceae,	204	Valerianaceae
168	Cornaceae		see Leguminosae	31	Velloziaceae
89	Crassulaceae	79	Monimiaceae	190	Verbenaceae
84	Cruciferae	170	Monotropaceae	147	Violaceae
206	Cucurbitaceae	52	Moraceae	129	Vitaceae
92	Cunoniaceae	87	Moringaceae	110	Vochysiaceae
6	Cupressaceae	34	Musaceae	22	Xyridaceae
1	Cycadaceae	46	Myricaceae	35	Zingiberaceae
18	Cyclanthaceae	78	Myristicaceae	103	Zygophyllaceae
16	Cyperaceae	174	Myrsinaceae		
118	Cyrillaceae	162	Myrtaceae		
112	Dichapetalaceae	10	Najadaceae		
135	Dilleniaceae	65	Nyctaginaceae		
32	Dioscoreaceae	71	Nymphaeaceae		
205	Dipsacaceae	137	Ochnaceae		
88	Droseraceae	56	Oleaceae		
178	Ebenaceae	181	Oleaceae		
156	Elaeagnaceae	164	Onagraceae		
130	Elaocarpaceae	57	Opiliaceae		
143	Elatinaceae	39	Orchidaceae		
172	Ericaceae	197	Orobanchaceae		
23	Eriocaulaceae	98	Oxalidaceae		

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*Field Museum of Natural History*

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## CONTENTS

LIST OF ILLUSTRATIONS.....	vi
ACKNOWLEDGMENTS .....	vii
PODOSTEMACEAE by William Burger (based on P. Van Royen).....	1
PROTEACEAE by William Burger .....	8
OLACACEAE by William Burger.....	14
OPIACEAE by William Burger .....	27
LORANTHACEAE (in a wide sense) by William Burger and Job Kuijt .....	29
EREMOLEPIDACEAE .....	31
LORANTHACEAE (in a narrow sense) .....	33
VISCACEAE.....	59
ARISTOLOCHIACEAE by Kerry Barringer.....	79
HYDNOACEAE by Luis D. Gómez .....	87
RAFFLESACEAE by Luis D. Gómez .....	89
BALANOPHORACEAE by Luis D. Gómez.....	93
POLYGONACEAE by William Burger.....	99
CHENOPODIACEAE by William Burger .....	138
AMARANTHACEAE by William Burger .....	142
NYCTAGINACEAE by William Burger .....	180
PHYTOLACCACEAE by William Burger .....	199
AIZOACEAE by William Burger.....	213
PORTULACACEAE by William Burger.....	217
BASELLACEAE by William Burger .....	222
CARYOPHYLLACEAE by Richard Baker and William Burger .....	227

## LIST OF ILLUSTRATIONS

1.	Podostemaceae .....	2
2.	Proteaceae .....	10
3.	Olacaceae and Opiliaceae .....	15
4.	Olacaceae: <i>Heisteria</i> .....	18
5.	Loranthaceae (s.s.): <i>Psittacanthus</i> and <i>Gaiadendron</i> .....	34
6.	Loranthaceae (s.s.): <i>Struthanthus</i> and <i>Phthirusa</i> .....	35
7.	Loranthaceae (s.s.): <i>Struthanthus</i> .....	36
8.	Loranthaceae (s.s.): <i>Oryctanthus</i> . Eremolepidaceae and Rafflesiaceae .....	37
9.	Viscaceae: <i>Dendrophthora</i> and <i>Phoradendron</i> .....	61
10.	Viscaceae: <i>Phoradendron</i> , second group .....	62
11.	Viscaceae: <i>Phoradendron</i> , third group .....	63
12a.	Aristolochiaceae: <i>A. maxima</i> and its allies .....	80
12b.	Aristolochiaceae: six species .....	81
13.	Hydnoraceae .....	88
14.	Rafflesiaceae: <i>Bdallophyton</i> .....	92
15.	Balanophoraceae: <i>Langsdorffia</i> and <i>Helosis</i> .....	94
16.	Balanophoraceae: <i>Corynaea</i> .....	95
17.	Polygonaceae: <i>Polygonum</i> .....	102
18.	Polygonaceae: <i>Rumex</i> .....	103
19.	Polygonaceae: climbing species .....	104
20.	Polygonaceae: species with winged fruit .....	105
21.	Polygonaceae: <i>Coccoloba</i> with rounded leaves .....	108
22.	Polygonaceae: <i>Coccoloba</i> with epistipular petioles .....	109
23.	Polygonaceae: <i>Coccoloba</i> with basal petioles .....	110
24.	Polygonaceae: <i>Coccoloba</i> , rarely collected species .....	111
25.	Amaranthaceae: <i>Achyranthes</i> and <i>Cyathula</i> .....	146
26.	Amaranthaceae: <i>Alternanthera</i> and <i>Gomphrena</i> .....	149
27.	Amaranthaceae: <i>Alternanthera</i> and <i>Pfaffia</i> .....	152
28.	Amaranthaceae: <i>Amaranthus</i> .....	158
29.	Amaranthaceae: <i>Celosia</i> , <i>Chamissoa</i> , and <i>Pleuropetalum</i> .....	163
30.	Amaranthaceae: <i>Iresine</i> .....	171
31.	Nyctaginaceae: <i>Bougainvillea</i> and <i>Mirabilis</i> .....	182
32.	Nyctaginaceae: <i>Boerhavia</i> and <i>Salpianthus</i> .....	183
33.	Nyctaginaceae: <i>Guapira</i> and <i>Pisonia</i> .....	184
34.	Nyctaginaceae: <i>Neea psychotrioides</i> complex .....	185
35.	Nyctaginaceae: <i>Neea amplifolia</i> complex .....	186
36.	Phytolaccaceae: <i>Microtea</i> , <i>Rivina</i> , and <i>Trichostigma</i> .....	200
37.	Phytolaccaceae: <i>Phytolacca</i> .....	201
38.	Phytolaccaceae: <i>Petiveria</i> and <i>Stegnosperma</i> . Chenopodiaceae .....	202
39.	Caryophyllales: succulent species .....	223
40.	Caryophyllales: Basellaceae and Portulacaceae .....	224
41.	Caryophyllales: herbs with narrow opposite leaves .....	225
42.	Caryophyllales: herbs with opposite or whorled leaves .....	226



## ACKNOWLEDGMENTS

This is the fourth issue of the *Flora Costaricensis*. The first dealt with Piperaceae (Fieldiana, Bot. 35, 1971), the second dealt with the families Chloranthaceae through Urticaceae (Fieldiana, Bot. 40, 1977), and the third dealt with Gramineae by Richard Pohl (Fieldiana, Bot., new series No. 4, 1980). In the work of preparing both this present volume and in all previous volumes, we have had the generous cooperation and support of the Museo Nacional de Costa Rica. Use of special facilities at the Museo for drying, processing, and shipping have been essential to our field program. Sr. Luis D. Gómez has been especially helpful to the flora program during the years he served as Director and since that time. Sr. Jorge Gómez-Laurito, associated with both the Herbario Nacional at the Museo Nacional and the Biology Department of the University, has also been most helpful.

We are especially grateful for the assistance of the National Science Foundation, Program for Systematic Biology, which has aided this program for many years. Financial support for fieldwork, assistants, and a postdoctoral position have been provided by NSF grants DEB 74-08575 and DEB 81-03184.



## PODOSTEMACEAE

REFERENCE: P. van Royen, The Podostemaceae of the New World, pt. 1, Meded. Bot. Mus. Herb. Rijks Univ. Utrecht 107:1–150, 1951. Part 2, Acta Bot. Neerl. 2:1–21. 1953.

Small herbs, growing in fast-moving freshwater rapids and waterfalls, usually attached to larger rocks (rarely wood), annual or perennial, bisexual, very variable in size and form, ranging from thalloid and closely attached to rocks to mosslike or with long branched leaves, sterile plants usually larger and thicker than the fertile, stems usually forming a broad holdfast and difficult to distinguish from the roots in some genera; lateral stipules or intrapetiolar stipules sometimes present. Leaves very different in different genera and species, in 2 or 3 ranks or borne from the edge or center of the thalloid stem, minute and appressed (in *Tristichia*) to large and much branched (in *Marathrum*). Inflorescences of solitary or fascicled pedicellate flowers, terminal, axillary or extra-axillary on special shoots or in 2-sided spikelike monochasia, each flower at first enclosed within a thin spathe or a few leaves or with groups of 10–20 flowers at first enclosed within a thickened spathe. Flowers bisexual, radially symmetrical or bilaterally symmetrical, very small (mostly less than 1 cm), borne on prominent pedicels often slightly expanded at the apex; perianth of 2 to many parts, in 1 or several whorls or on only 1 side, either thin and petal-like or reduced to small scales, free or united at the base; stamens 1 to many, often alternate with the perianth parts (tepals) in 1 or 2 whorls, in a whorl or on only 1 side of the flower, filaments free or united (rarely on an andropodium), anthers opening by 2 longitudinal slits, introrse or extrorse, basifixed or dorsifixed; ovary superior, narrowed at the base or on a short stalk, sometimes obliquely oriented in the flower, 1- to 3-locular, placentation axile with 2 to many anatropous ovules, styles (1) 2 or 3, usually slender. Fruit a thin-walled capsule, seeds 2 to many, without endosperm, embryo straight.

A family of about 200 species in 43 genera, pantropical but reaching the middle Atlantic states of the United States and Japan in the Northern Hemisphere and northeastern Australia in the Southern Hemisphere. This is one of the most unusual families of angiosperms, both in morphology and in habitat. Because of their restriction to fast-moving water, these plants are difficult to collect, and our knowledge of them is poor. Fortunately, we have the excellent monograph by van Royen covering the American genera and species (see the references above). Nearly all of this treatment is based on van Royen's work, but it may be that some of his species of *Marathrum* were circumscribed too narrowly.

### KEY TO THE GENERA OF PODOSTEMACEAE

- 1a Leaves minute (to 4 mm), in 3 imbricate ranks on short erect stems and resembling bryophytes; young flowers protected by a few leaves, with 3–5 broad perianth parts; ovary 2- or 3-locular. .... *Tristichia*
- 1b Leaves 1–50 cm long, cuneate to much branched and divided or tripinnate, borne on flat thalloid stems and resembling algae; young flowers enclosed in a narrow spathe, perianth parts very narrow or minute and scalelike; ovary 1- or 2-locular

*Marathrum*



FIG. 1. Podostemaceae: species of *Marathrum* and *Tristichia trifaria*, lower left, enlarged.

## MARATHRUM Humboldt and Bonpland

Small aquatic herbs attached by a broad irregular base to rocks in fast-moving water, glabrous, bisexual, sterile plants often larger than the fertile, the stem often difficult to distinguish from roots or leaf bases; an intrapetiolar stipule or ligule often present. Leaves variously inserted on the thalloid base or distichous, very variable in size and form, from subentire with a few distal lobes to repeatedly forked or repeatedly pinnate and branch-like, conforming to the flow of water or prostrate on the rocks, petiole and rachis often fleshy. Inflorescences of solitary or fascicled flowers arising from between the leaf bases, each flower at first enclosed within a translucent tubular-clavate spathe which splits irregularly near the apex, pedicels becoming elongate and often slightly expanded at the apex; flowers bisexual, radially symmetrical (stamens and perianth on only 1 side in *M. tenue*), perianth of 3–25 parts in 1 or several whorls or on only 1 side, lanceolate to linear or filiform or reduced (0.3 mm) and scalelike at the base of the flower, free or united at the base, sometimes inserted on the cuplike apex of the pedicel; stamens 2–25, whorled or on only 1 side, united only at the base, filaments linear to lanceolate, anthers introrse; ovary superior and 2-locular, usually ellipsoid and narrowed at the base, with 6 or 8 longitudinal ribs, styles 2, free or united near the base. Fruit a capsule, splitting along the longitudinal ribs to produce 2 equal halves each with 5 ribs, seeds small and numerous.

*Marathrum* includes about 20 to 25 species, ranging from Mexico and Cuba through Central America to northwestern South America where the genus intergrades with *Apinagia* (see van Royen, 1951). Different species have leaves that vary from short, simple, and rhombic or flabellate to much longer and divided or compound-pinnate, but the flowers and fruit seem quite similar. Standley noted that the name *Pasacarne* has been used for these plants in Costa Rica and that cattle will wade out into stream rapids to feed on them in the dry season (see Fieldiana, Bot. 24, pt. 4:402, 1946). Fertile material has only been collected in the dry season, from early January to middle May.

While appreciative of van Royen's excellent monograph, I believe that some of his species are separated on rather minor characters. Nevertheless, it seemed important to provide the user of this flora with the distinctions that van Royen used to separate species. Accordingly, the key utilizes van Royen's dichotomies for all the species of Costa Rica and adjacent areas, but the last five species in the key are probably covered under the expanded description of *M. oxycarpum*. In his monograph of 1951, van Royen had already submergered some of the species he described for the Flora of Panama (Ann. Missouri Bot. Gard. 37:126–137, 1950); see the discussion under *M. oxycarpum*.

KEY TO THE COSTA RICAN SPECIES OF *Marathrum*  
BASED ON THE KEY OF VAN ROYEN (1951)

- 1a Leaves cuneate or somewhat flabellate, relatively broad (2–30 mm), lobed or pinnatisect only distally, with distinct reticulate venation when dry . . . . . *M. utile*
- 1b Leaves with a central narrow (1–4 mm) rachis or much divided from near the base, often twice pinnatifid and branchlike in appearance, without broadly reticulate venation . . . . . 2a
- 2a Stamens and perianth parts 2 or 3, borne on 1 side of the flower, apex of the pedicel often becoming asymmetric in fruit with ribs of the fruit decurrent into the pedicel on 1 side; anthers 1 mm long or less; ultimate divisions of the leaf short and very slender, producing a characteristically "fimbriate" ultimate cluster . . . . . *M. tenue*
- 2b Stamens and perianth 5–10 or more, in whorls around the flower and fruit; apex of the pedicel not strongly asymmetric; anthers to 2 mm long; distal leaf segments not usually densely fimbriate with short filiform divisions . . . . . 3a
- 3a Pedicel usually becoming broadened and cuplike at the apex . . . . . 4a
- 3b Pedicel only slightly enlarged at the apex, never forming a cuplike base for the flower . . . . . 5a

- 4a Leaf segments repeatedly forked, with long (0.5–12 mm) and very slender terminal divisions, never pinnatisect in appearance; rare in Central America *M. foeniculaceum*
- 4b Leaf segments usually in alternate arrangements on the central rachis and giving a pinnatifid appearance, ultimate division 1–3 mm broad or if slender not usually exceeding 5 mm in length; common in Central America but may intergrade with *M. oxycarpum* ..... *M. schiedeianum*
- 5a Fully developed stamens about half as high as the ovary; not recorded from Costa Rica: *M. stenocarpum* (Weddell) van Royen, Panama and Colombia.
- 5b Fully developed stamens more than half as high as the ovary, usually equalling or exceeding the ovary in height; all the following species (as separated by van Royen) seem very similar, and a description is provided only for *M. oxycarpum* in a wider sense. .... 6a
- 6a Styles filiform, widened at the top; sometimes emarginate, 2–3 mm long, cohering over a long distance; stamens 8–10; ultimate divisions of the leaf up to 3 cm long (= 3 mm?) and up to 0.3 mm wide ..... *M. oxycarpum*
- 6b Styles of different shape, cohering at the base only, up to 2 mm long; stamens 5–9; ultimate divisions of the leaf 5 mm long or less ..... 7a
- 7a Largest leaves shorter than 7 cm long ..... 8a
- 7b Largest leaves up to 30 cm long. .... 9a
- 8a Leaves repeatedly pinnate, 3–6 cm long; styles filiform, up to 1 mm long; pollen grains  $20 \times 11 \mu\text{m}$ : *M. leptophyllum* van Royen, western Panama.
- 8b Leaves repeatedly pinnate or cuneate and dissected at the top, up to 1 cm long; styles cylindrical, ca. 1.5 mm long; pollen  $15 \times 14 \mu\text{m}$ : *M. pusillum* van Royen, central Panama.
- 9a Leaves without an intrapetiolar stipule at the base ..... *M. cheiriferum*
- 9b Leaves with an intrapetiolar stipule at the base ..... *M. minutiflorum*

**Marathrum cheiriferum** van Royen, Ann. Missouri Bot. Gard. 37:134–135. 1950.

It is very difficult to see the intrapetiolar stipules on many specimens of *Marathrum*, and to use such a characteristic to separate species seems impractical. In addition, the separated specimens seem so similar in other aspects of both vegetative and floral morphology that one doubts they are different species. Costa Rican material identified as *M. cheiriferum* by van Royen is tentatively being placed under *M. oxycarpum* in a wide sense (q.v.).

**Marathrum foeniculaceum** Humboldt and Bonpland, Plantae Aequin. 1:40–41, t. 11. 1808. *Lacis foeniculacea* (H. & B.) Martius, Nov. Gen. & Sp. 1:6. 1824.

Aquatic herbs to 50 cm long, attached by an irregular base to 2 cm broad; intrapetiolar stipules present, to 3 mm high. Leaves repeatedly divided or forked (rarely repeatedly pinnate in early stages), 2.5–50 cm long, petiole flattened, 1–8 cm long, widened at the base, ultimate divisions usually very slender and without a midvein, to 15 mm long. Flowers solitary or fascicled, spathe up to 15 mm long, pedicels up to 35 mm long and expanded at the apex to form a broad shallow cup; perianth parts 5–8, linear, ca. 1 mm long, arising from the edge of the disklike pedicel apex; stamens 5–8, 4–6 mm long, anthers ca. 1 mm long; ovary 3–4.5 mm long, 1–1.5 mm in diameter, styles 1–2.5 mm long. Fruit ca. 4.5 mm long, each valve with prominent ribs.

This species ranges from Belize to Colombia, but has not been collected from Costa Rica.

*Marathrum foeniculaceum* is characterized by the pedicels expanded at the apex to form a shallow "floral" cup and the relatively long slender distal divisions of the leaves which obscure the pinnate form of the leaf and give the leaf a more alga-like appearance. This leaf form is quite distinctive and unlike that of other species of *Marathrum* in our area.



***Marathrum minutiflorum*** Engler, Bot. Jahrb. Syst. 61, Beibl. 138:4. 1927. *M. allenii* Woodson, Ann. Missouri Bot. Gard. 25:827–828. 1938. *M. indifferens* van Royen, loc. cit. 37:132–133. *M. minutiflorum* forma *allenii* (Woods.) v. Royen, Meded. Bot. Mus. Herb. Rijks Univ. Utrecht 107:80. 1951. *M. minutiflorum* forma *diversifolium* v. Royen, loc. cit. 81. *M. minutiflorum* forma *indifferens* (v. Royen) v. Royen, loc. cit. 81. *M. minutiflorum* forma *intermedium* v. Royen, loc. cit. 81.

At present, it seems best to interpret material placed under the above names by van Royen (1951) as robust specimens of *M. oxycarpum* in a wide sense; see the description and discussion under *M. oxycarpum*.

***Marathrum oxycarpum*** Tulasne, Ann. Sci. Nat. Paris, ser. 3, 11:94–95. 1849.

Small- to medium-sized herbs, 2–50 cm long, base with an irregular shape, ca. 1 cm wide and to 3 cm long; intrapetiolar stipules usually present. Leaves usually 3 × pinnate, 3–20 (50) cm long, petiole terete or compressed, to 12 cm long, pinnae alternate on the rachis, ascending, ultimate divisions of the leaf spatulate (rarely filiform). Flowers solitary, at first enclosed in a tubular spathella to 12 mm long, pedicels slightly thickened at the apex but never forming a cup, to 5 (9?) cm long; perianth parts 5–10, 1–3 (4) mm long, narrowly lanceolate; stamens 5–10, 2.5–4.5 (6) mm long, anthers 1–2 mm long; ovary 2–4 mm high, 1–2 mm in diameter, with 8 distinct longitudinal ribs, styles 1–3 mm long, slender. Fruit 2.5–5 mm long, the smaller rounded and obtuse at the apex and the longer more ellipsoid, each valve with 5 prominent ribs.

Aquatic plants of rocky streams growing at or up to 1 m below the water level. Ranging from near sea level to 1,200 m elevation in Costa Rica and flowering from January to May. Most collections are from the Pacific slope, but a few come from the Caribbean watershed. This species, defined in a wider sense, ranges from Mexico to Colombia.

*Marathrum oxycarpum* is recognized by its distally slender pedicel, whorled perianth and stamens, strongly ribbed fruit, and its complex tripinnate leaves. This species may be polymorphic, with some plants (often collected without leaves) producing smaller, often stalked round fruit and other plants (usually leafy) producing larger (3.5–5 mm) sessile ellipsoid fruit. These latter plants look similar to specimens of *M. schiedeanum*, with some individuals actually having an expanded pedicel apex. Some plants have large (2 mm) anthers, but with other floral characters being typical. The minute perianth parts at the base of the flower (and alternating with the longer narrow perianth parts) are often conspicuous in this species. All perianth parts may be deciduous before the fruit is mature.

*Marathrum oxycarpum*, as here defined, may be something of a catchall, since the more distinctive entities of the genus are separated in the earlier dichotomies of the key to species. Nevertheless, the material identified by van Royen as *M. cheiriferum* and *M. minutiflorum* seems to fall into this assemblage very naturally; all these plants seem to share exactly the same altitudinal range, and their inclusion in one species gives a more evenly distributed pattern of collecting localities through Central America. Perhaps *M. leptophyllum* and *M. pusillum* of Panama belong here as well (see the key). This larger circumscription of *M. oxycarpum* also allows us to identify the small-fruited material lacking well-developed leaves which may represent late-flowering plants (in respect to local water level) that are less robust. Another reason for the broader interpretation of this species is that one does not expect so many similar sympatric species in a genus whose life-style is so specialized and so dependent on effective dispersal. See the discussion under *M. schiedeanum*.

**Marathrum schiedeanum** (Cham.) Tulasne, Ann. Sci. Nat. Paris, ser. 3, 11:95. 1849. *Lacis schiedeanum* Chamisso, Linnaea 9:504–505, t. 566. 1835. *Marathrum flexuosum* Liebmann, Föhr. Skand. Naturf. 5:511. 1849. Figure 1.

Aquatic herbs to 50 cm long, base irregular, to 2 cm wide; intrapetiolar stipules usually present, 1.5 mm long, obtuse. Leaves up to 50 cm long, repeatedly pinnate, the young leaves sometimes repeatedly divided, petiole terete or slightly flattened, 0.5–13 cm long, pinnae usually ascending, ultimate divisions of the leaf to ca. 3 mm long and varying from 2–3 mm broad to filiform, acute to obtuse at the apex, with or without a midvein. Flowers solitary or fascicled, spathella 1–1.5 cm long, pedicels 1–4 (9) cm long, expanded at the apex and forming a distinctive shallow or deep (2 mm) cup, 2 mm broad at the apex; perianth parts 5–8, linear to lanceolate, 0.5–1.5 mm long; stamens 5–8, 3.5–4.5 mm long, anthers ca. 1 mm long; ovary 2–5.5 mm long, 1.5–3 mm in diameter with 8 longitudinal ribs, styles 1–2 mm long. Fruit to 5.5 mm long and 3 mm thick, ellipsoid, each valve with 5 prominent ribs.

This species is found from near sea level to 1,200 m elevation on the Pacific slope and ranges from Mexico to southern Costa Rica; it flowers and fruits from January to May.

*Marathrum schiedeanum* is characterized by the pedicel expanded at the apex to form a “floral” cup from which the perianth and stamens arise and the often large tripinnate leaves with ultimate divisions that may be broad and pinnatifid or slender and filiform. This species may hybridize or intergrade with *M. oxycarpum*. An alternative interpretation is that the cupulate nature of the pedicel apex is not a character worthy of distinguishing species in this instance; the character seems variable in some collections and there do appear to be intermediate individual collections, such as *Bunting & Licht 1018* from Nicaragua. It may be that all the material under both *M. oxycarpum* in its expanded circumscription and *M. schiedeanum* is part of a single polymorphic species. For this reason, it seems best to place sterile material under the oldest name (*M. schiedeanum*), but to continue to use the pedicel apex to distinguish fertile material into two species.

**Marathrum tenue** Liebmann, Föhr. Skand. Naturf. 5:511. 1849. *Neolacis myriophylla* Weddell, in DC., Prodr. 17:63–64. 1873. *Blandowia myriophylla* (Wedd.) Nash, N. Amer. Fl. 22, pt. 1:5. 1905. *Apinagia myriophylla* (Wedd.) Engler, Natur. Pflanzenfam. 18a:38. 1930. Figure 1.

Small aquatic herbs to 20 cm long, from a flat or branched base to 1.5 cm high; stipules absent but the petioles sheathing at the base. Leaves repeatedly pinnate, central rachis to 15 (20) cm long, petiole usually terete and up to 6 cm long, ultimate divisions filiform and less than 2 mm long and resulting in distinctive densely 3-dimensional pinnae. Flowers solitary or fascicled, spathellae 3–10 mm long, pedicel to 2.5 cm long, somewhat asymmetric at the apex or becoming asymmetric; perianth parts 2, 3, or 4, on 1 side of the flower, lanceolate to filiform, to 1.5 mm long; stamens 2 or 3, 2.5–4.5 mm long, filaments lanceolate (resembling perianth parts), anthers 1–1.5 mm long; ovary 2–3 mm long, 1–2 mm in diameter, styles ca. 1 mm long. Fruit ca. 3 mm long, strongly ribbed with the ribs on the side of the flower lacking perianth and stamens often decurrent on the pedicel, each half of the fruit with 5 prominent ribs or with 3 prominent and 2 less prominent ribs.

Usually submerged aquatic plants growing on rocks in fast water and flowering in the dry season, January to May. The species is found from near sea level (100 m) to 1,600 m elevation in Costa Rica, but has only rarely been collected below 1,000 m elevation. The species ranges from Mexico to Costa Rica and is to be expected in western Panama.

*Marathrum tenue* is distinguished by the small number of stamens and perianth parts arising on only one side of the flower. Because of this asymmetry, the apex



of the pedicel is usually enlarged on one side, and the ribs of the fruit are often decurrent into the pedicel on the opposite side; no other species in our area has similar flower and fruit. In addition, the leaves with prominent central rachis and alternate pinnae with numerous (often closely crowded) ultimate divisions are quite different from typical leaves of the other species in our area.

**Marathrum utile** Tulasne, Ann. Sci. Nat. (Paris), ser. 3, 11:95. 1849. Figure 1.

Small aquatic herbs, to 35 cm long, base ca. 2 cm long, shoots opposite along the root but difficult to see. Leaves 3–35 cm long, 1–6 cm broad, often rhombic when young, becoming spatulate to cuneate, entire to pinnatisect or palmisect distally, the distal lobes or segments usually few (2–8), broad areas of the leaf with distinctive venation (dichotomous and reticulate), the lamina gradually narrowed to the base and the petiole not clearly differentiated. Flowers solitary or in fascicles, spathe 2–2.5 cm long, pedicels 1–4 cm long, expanded distally and forming a short broad cup; perianth parts 5–8, up to 2 cm long (difficult to distinguish from the filaments); stamens 5–8, 2–5.4 mm long, anthers 1–1.5 mm long; ovary 2–4 mm long, ellipsoid to ovoid, style 1.5–2 mm long. Fruit to 4 mm long, with conspicuous longitudinal ribs.

Herbs growing in the fast water of streams and known only from the Pacific slopes of the Cordillera Central and Cordillera de Talamanca between 1,000 and 2,000 m elevation in Costa Rica. The species is known from Costa Rica, Colombia, and Panama.

*Marathrum utile* is immediately distinguished by its broad laminae with anastomosing venation and divided only near the apex. The pedicels slightly cupulate at the apex are also distinctive. Although only collected above 1,000 m in Costa Rica, this species is known from lower elevations in Colombia.

#### TRISTICHA Du Petit-Thouars

Bryophyte-like herbs, forming dense mats on rocks in fast-moving water, stems thin and terete, glabrous, bearing leaves on 3 sides; stipules absent. Leaves alternate and in 3 ranks or becoming whorled in groups of 3 or 6, subsessile, lamina small and usually imbricate, entire or divided at the tip, with or without a midvein. Inflorescences absent, the flower solitary and terminal on the main stems or on short lateral shoots, young flower buds protected by 2 or 3 distinctly larger overlapping leaves, pedicels long and slender; flowers small and radially symmetrical, perianth 3-parted, free or united into a 3-lobed tube; stamen 1, filament slender, anthers introrse with an elongate connective; ovary 3-locular, with 3 slender erect styles. Fruit a capsule dehiscent by 3 equal valves, each valve with 3 ribs, seeds numerous.

A genus of three species in tropical and subtropical America, Africa, and Asia. Only one species is known to occur in the Americas. Like other members of the family, these plants are found only in fast-moving fresh water, and they resemble mosses and leafy liverworts more than they do flowering plants; even the little flowers and fruits resemble the stalked capsules of mosses.

**Tristicha trifaria** (Bory ex Willd.) Sprengl, Syst. Veg., ed. 16, 1:22. 1825. *Dufourea trifaria* Bory ex Willd., Sp. Pl., ed. 5:55. 1811. *Dufourea hypnoides* St. Hil., Mém. Mus. Hist. Nat. 10:472. 1823. *Tristicha hypnoides* (St. Hil.) Sprengl, Syst. Veg. 4, pt. 2:10. 1827. *T. trifaria* (Bory ex Willd.) Tulasne, Arch. Mus. Hist. Nat. 6:179. 1852. Figure 1.

Small herbs, 1–4 (10) cm high, mosslike and firmly attached to rocks, often forming dense mats, stems often numerous, terete, leafy stems 1–3 cm long; without stipules. Leaves very small and overlapping on the stem, often somewhat dimorphic, with those on the upper stems 0.3–1 mm long and ovate, those of the lower stems to 0.4 mm broad and

2 mm long and spatulate in form, apex of the lamina entire or rarely split into 2–4 acute lobes, glabrous. Flowers at first enclosed within 2 or 3 larger leaves, borne on a slender pedicel 3–10 (20) mm long; perianth of 3 free or united petals, 1–2 mm long, perianth lobes obtuse; stamen 1.5–2.5 mm long, anthers ca. 0.8 mm long; ovary 0.5–1 mm long and ca. 0.8 mm in diameter, ellipsoid, rounded or narrowed at the base, styles ca. 0.5 mm long. Fruit an ellipsoid thin-walled capsule, ca. 1.5 mm long, with prominent longitudinal ribs.

Aquatic plants attached to rocks in fast-flowing freshwater streams from near sea level to 1,300 m elevation; flowering and fruiting from January through April in Costa Rica. The plants also flower in November and December in El Salvador and Nicaragua where the dry season may begin earlier. They are found on both the Pacific and Caribbean slopes. The species ranges from Cuba and southern Mexico to Colombia, Venezuela, Brazil, Uruguay, and northern Argentina.

*Tristicha trifaria* is recognized by its small bryophyte-like stems, with three ranks of very small leaves attached by holdfasts to rocks in rapidly moving water. The small flowers and ellipsoid fruit borne on a slender pedicel resemble the stalked capsule of a moss.

### PROTEACEAE

REFERENCE: H. Sleumer, *Proteaceae americanae*. Bot. Jahrb. Syst. 76:139–211. 1954.

Trees or shrubs (in ours), usually bisexual; stipules absent. Leaves simple or compound, the juvenile leaves often pinnately compound and the mature foliage often simple, alternate in a spiral to opposite or whorled (sometimes on the same stem), the laminae usually stiff and drying coriaceous, entire to serrate or pinnately lobed. Inflorescences racemes, spikes, umbels, or heads, rarely with flowers solitary or paired; flowers radially or bilaterally symmetrical, perianth of 1 outer whorl of usually 4 parts, free or united, valvate and tubular but splitting apart at the apex and usually becoming recurved, sometimes splitting on only 1 side; stamens opposite the perianth parts and the filament often adnate to them, the anthers introrse and often exposing the pollen to the air or transferring pollen to the style prior to pollination, an inner whorl of perianth-like nectar scales of hypogynous disk elements usually present around the base of the ovary; pistil superior and often short-stipitate, solitary, 1-carpellate, ovary with 1 locule and 1 to many ovules, style solitary and unbranched with a thickened or enlarged stigma. Fruit usually woody, splitting open (a follicle) or remaining closed (a nut) with 1 to many seeds; seeds flattened or round, sometimes winged, the cotyledons often unequal, lacking endosperm.

A moderately large family of about 60 genera and a little more than 1,000 species largely restricted to the warmer portions of the Southern Hemisphere. The family is best represented in Australia and southern Africa, especially in areas marked by a long dry season. A number, such as *Banksia* and *Protea*, are cultivated in the subtropics for their spectacular inflorescences. The stiff foliage usually evergreen and often with both pinnate and simple leaves on different parts of the same plant help to distinguish these woody plants. The usually narrow-tubular flower buds with four valvate perianth parts, perianth-opposing stamens, and one-locular pistils with simple style and stigma further distinguish the family. These plants may resemble some members of the Loranthaceae which have inferior ovaries and are often parasitic.

- 1a Introduced plants of gardens and roadsides; mature leaves pinnate or deeply pinnatifid, alternate along the stem, (simple leaves absent); flower buds bent backward and somewhat U-shaped ..... *Grevillea*
- 1b Native plants of forest and woodland; mature leaves usually simple, alternate to opposite or whorled on the stems (pinnately compound leaves present or absent); flower buds straight ..... 2a

- 2a Leaves isomorphic, always simple and entire, the tertiary veins becoming prominent on both surfaces when dry; anthers borne on prominent filaments; fruit round and not splitting open ..... *Panopsis*
- 2b Leaves heteromorphic, immature and flowerless shoots usually with pinnately compound leaves and mature or flowering shoots usually with simple leaves; anthers sessile or subsessile on the perianth parts; fruit somewhat flattened and splitting open along the edge ..... *Roupala*

### GREVILLEA R. Brown

Shrubs or trees, bisexual, evergreen. Leaves alternate, simple to pinnately compound or pinnately divided. Inflorescences usually terminal, racemes or umbels, flowers in pairs along the rachis, with hairs usually attached in the middle; flowers bisexual, radially or bilaterally symmetrical, the perianth tube straight and slender or curved, the apical part of the perianth usually expanded and bearing the sessile stamens, anthers ovate, the connective not produced beyond the anthers, hypogynous disk usually a single semi-circular gland on the upper side of the receptacle or rarely completely circular or absent; ovary usually stipitate, the 2 ovules attached laterally near the middle of the locule wall, style filiform, often protruding from the slit in the underside of the perianth tube before the perianth opens completely, stigma on the terminally expanded style. Fruit a follicle, coriaceous or woody, often with the long style persisting, usually opening along the upper margin; seeds flat or round, usually bordered by a wing.

A primarily Australian genus of about 190 species. Two species are widely planted in the tropics and in Central America. They have large (12 to 35 cm) pinnate or pinnatifid leaves, colorful racemes, and small (2 cm) follicles splitting open along one side.

- 1a Trees to 20 (30) m tall, often planted along avenues and in parks; leaves pinnate with pinnatifid pinnae; flowers orange; fruit glabrous ..... *G. robusta*
- 1b Shrubs or small trees to 7 m tall; leaves pinnate or once pinnatifid; flowers red; fruit villous ..... *G. banksii*

**Grevillea banksii** R. Brown, Trans. Linn. Soc. 10:176. 1810.

Tall shrubs or slender trees to 7 m tall, branches and inflorescences reddish brown tomentulose. Leaves pinnate or pinnatifid, 10–20 cm long, with 3–11 linear or lanceolate segments, 5–10 cm long, margins entire and revolute. Flowers red to rose red, in compactly flowered racemes 5–12 cm long, pedicels ca. 5 mm long, perianth tube strongly recurved below the apex, ca. 1.5 cm long, densely puberulent; fruit ca. 1.5 cm long with a long (4 cm) persisting style.

Usually planted in gardens and near houses.

**Grevillea robusta** Cunningham, in R. Br., Prot. Nov. 24. Figure 2.

Small and slender to large and robust trees, branches and inflorescences pale grayish to orange-brown tomentulose. Leaves usually pinnate, 15–30 cm long with ca. 10–20 pinnatifid leaflets, pinnae or leaflets ca. 5–10 cm long, margins usually lobed and revolute. Flowers orange, in loosely flowered racemes 10–20 cm long, pedicels ca. 1.5 cm long, perianth tube strongly recurved at about the middle, 1 cm long (2 cm measured along the curve); fruit ca. 2 cm long.

Often planted in parks and along streets and avenues.

### PANOPSIS Salisbury

Trees, bisexual, the foliage monomorphic. Leaves alternate, subopposite, opposite, or whorled, simple, entire, drying coriaceous. Inflorescences terminal or axillary, usually solitary, racemose with many flowers, the flowers arising solitary, 2, or 3 together on the rachis, with or without bracts; flowers bisexual, radially symmetrical, the perianth cylin-

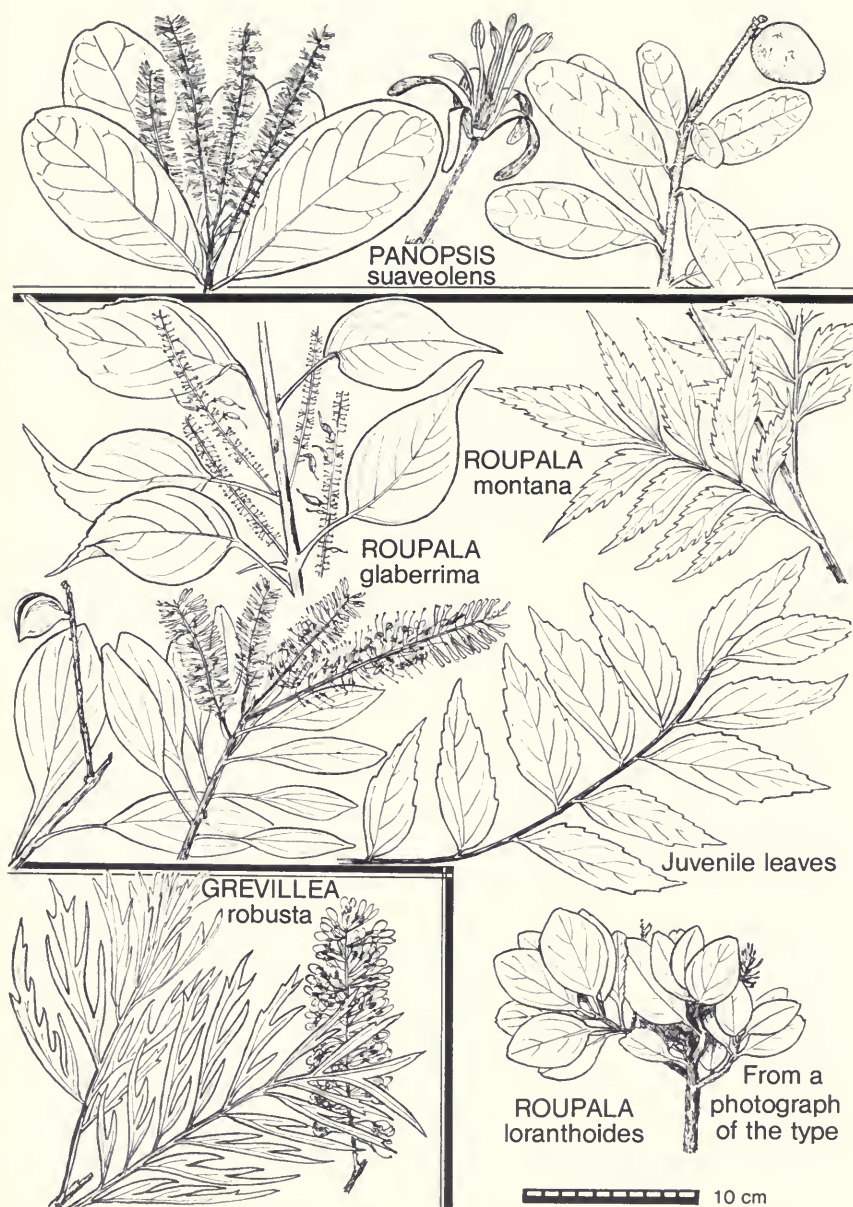


FIG. 2. Proteaceae: a cultivated species of *Grevillea* and native species of *Roupala* and *Panopsis*. Note: reduced scale.



drical and straight in bud, separating at anthesis into 4 perianth parts (tepals), the tepals free to the base and becoming recurved; stamens arising from the lower half of the tepals or from their base, filaments largely free, anthers oblong, connective apiculate; hypogynous disk a thin 4-lobed cup resembling a short perianth tube; ovary subsessile, ovules 2, pendulous, stigma terminal. Fruit indehiscent with a thick woody pericarp, seeds lacking wings, rounded.

An American genus of about 11 species ranging from Costa Rica southward to Peru, Bolivia, and Brazil. The lack of pinnate leaves on younger parts, racemose flowers with distinct filaments, and the hard fruit that do not split open distinguish this genus from other Proteaceae.

**Panopsis suaveolens** (Kl. & Karst. ex Klotzsch) Pittier, Contr. Fl. Venez. 22. 1923. *Andripetalum suaveolens* Klotzsch & Karsten ex Kl., Linnaea 20:472. 1847. *Panopsis costaricensis* Standl., J. Wash. Acad. Sci. 17:164. 1927. Figure 2.

Trees 5–15 (25) m tall, trunks to 80 cm in diameter, with brown bark, leafy internodes (1) 5–30 mm long, 2–5 mm thick, reddish brown strigulose at the nodes but soon becoming glabrous, with conspicuous lenticles 0.3–1 mm long, axillary buds densely covered with lustrous reddish brown hairs. Leaves alternate to opposite, often clustered near the ends of branchlets, petioles 2–12 mm long, 1–2 mm thick, striate and glabrous; laminae (3) 5–15 (17) cm long, (1.3) 2–6 (9) cm broad, narrowly oblong to elliptic or narrowly to broadly obovate, bluntly obtuse and rounded at the tip, obtuse to cuneate at the base and somewhat decurrent on the petiole, margins entire or slightly undulate, lamina drying very stiffly chartaceous to subcoriaceous, smooth and glabrous on both surfaces when mature, often lustrous, the 4–8 pairs of major secondary veins arising at angles of 30°–65°, arcuate and weakly connected near the margin, tertiary veins raised and prominent on both surfaces (dry). Inflorescences axillary or in terminal clusters, always near the ends of stems, 6–16 cm long, racemes with more than 30 flowers each, rachis with slender ascending yellowish brown hairs 0.1–0.5 mm long, pedicels 2–5 mm long, densely appressed puberulent, perianth 6–7 mm long, sparsely puberulent; filaments 4–5 mm long, anthers ca. 1.5 mm long with a slender apiculate connective, hypogynous disk forming a thin cup or tube 0.5–0.7 mm long, enclosing the base of the ovary and mostly glabrous; ovary ca. 1.5 mm long, densely covered with hirsutulous orange-brown hairs to 0.5 mm long, style ca. 5 mm long. Fruit indehiscent, a very hard woody nut, 3.5–6 cm long and becoming 4.5 cm in diameter, ellipsoid to ovoid or subglobose, narrowed at the base and apex, the surface smooth and glabrous, dark brown with paler markings.

Trees of the very wet forests along the Continental Divide and the Caribbean slopes between 1,000 and 2,200 m elevation in Costa Rica; flowering from April to July and fruiting from July to March. The species ranges from central Costa Rica southward to Colombia, Venezuela, and Ecuador.

*Panopsis suaveolens* is recognized by its glabrous leaves with prominent tertiary venation that are alternate, subopposite, or opposite, often on the same stem. The puberulent racemes with many flowers and hard round fruit that do not open further distinguish the species. The trees have been called *Palo de papa* and *Papa* in Costa Rica and *Aguacatia* in Panama.

#### ROUPALA Aublet

Shrubs or trees, bisexual, the juvenile and sterile shoots usually with pinnately compound leaves and the flowering branches usually with simple foliage. Leaves heteromorphic with both pinnately compound and simple leaves, alternate in a spiral to subopposite or opposite, the laminae very stiff, dentate to entire with the pinnate leaves usually dentate. Inflorescences axillary or terminal, spikes or racemes, flowers often arising 2 or 3 together on the rachis; flowers bisexual and radially symmetrical, the perianth cylindrical and straight in bud, separating at anthesis into 4 perianth parts (tepals), the tepals free to the base and becoming recurved; stamens adnate to about the middle of the

tepals, the filament almost entirely adnate, anthers linear-oblong, sessile or subsessile, connective slightly prolonged beyond the thecae, a hypogynous disk or perianth-like whorl of flat scales or glands present at the base of the pistil; ovary with 2 pendulous ovules, stigma terminal. Fruit a short-stipitate follicle with thick hard walls, splitting obliquely into 2 flattened or slightly rounded valves, the seeds winged.

An American genus of about 50 species ranging from southern Mexico southward to Peru, Bolivia, and Rio Grande do Sul, Brazil. Three species have been reported from Costa Rica. The very stiff often heteromorphic leaves, glabrous except at the base of the petiole in the leaf axil, and often alternate to subopposite, help to distinguish these woody plants.

- 1a Inflorescence and flowers sparsely puberulent, perianth parts 7–9 mm long; simple leaves long-acuminate; fruit ca. 3.5 cm long; trees and shrubs of the seasonally dry Pacific slope, 40–1,200 m elevation. . . . . *R. montana*
- 1b Inflorescence and flowers glabrous (in ours); trees of moist cloud forests and evergreen montane forests. . . . . 2a
- 2a Simple leaves on mature shoots with laminae 5–15 cm long and with acuminate apices; perianth parts 10–14 mm long; fruit ca. 4 cm long; trees of wet evergreen forests (800) 1,500–2,500 m elevation. . . . . *R. glaberrima*
- 2b Simple leaves on mature shoots with laminae 3–7 cm long and with bluntly obtuse or rounded apices; perianth parts 7–9 mm long; fruit unknown; habitat unknown but may be exposed ridges and montane wind gaps . . . . . *R. loranthoides*

***Roupala glaberrima*** Pittier, Contr. U.S. Natl. Herb. 18:299. 1917. Figure 2.

Trees 5–20 (30?) m tall, bark gray, leafy internodes 3–30 mm long, 1–5 mm thick, very minutely puberulent but soon becoming glabrous, grayish. Leaves alternate, subopposite, or occasionally opposite, heterophyllous and pinnately compound on the young shoots or simple, rarely pinnate on the flowering shoots, simple leaves with petioles 1–8 cm long, 1–2 mm thick, very minutely puberulent near the base adaxially but glabrous elsewhere, simple leaves with laminae 5–15 cm long, 2.5–6 cm broad, narrowly ovoid to rhombic or obovate in outline but very variable (often on the same twig), gradually tapering to an obtuse to acuminate or caudate-acuminate apex, occasionally rounded or slightly emarginate at the tip, abruptly to gradually narrowed below the middle but decurrent and forming small winged margins on the petiole, margin entire to undulate or bluntly dentate, the laminae drying subcoriaceous, smooth and glabrous on both surfaces, usually slightly lustrous above, the 2–4 pairs of major secondary veins arising at angles of 15–35 degrees from the proximal half of the midvein, secondary veins slightly raised beneath (dry), tertiary veins obscure. Inflorescences usually solitary in the axils of persisting leaves, 8–22 cm long, racemose with more than 40 flowers, rachis glabrous and ca. 1 mm thick (dry), pedicels 3–7 mm long, ca. 0.5 mm thick; perianth parts 10–14 mm long, ca. 1 mm broad, linear oblanceolate, glabrous, white when flowering; anther ca. 3 mm long on a filament 1 mm long borne on the upper third of the tepal, hypogynous glands ca. 0.5 mm long, rounded apically; pistil ca. 10–11 mm long with the ovary 1 mm long and glabrous. Fruit ca. 4 cm long and 2 cm broad, flattened and asymmetrically obovate, abruptly narrowed at apex and base, opening distally and along one side, surface smooth and glabrous; seeds not seen.

Trees of the wet cloud forests along the Continental Divide and adjacent areas on both the Pacific and Caribbean slopes between (800) 1,500 and 2,500 m elevation; flowering from March to July and fruiting from October to February in Costa Rica. The species ranges from El Salvador to the western part of the Cordillera de Talamanca. The species is apparently rare east of Volcan Barba.

*Roupala glaberrima* is recognized by the stiff leaves that are pinnately compound on juvenile shoots but usually simple and long-petiolate on flowering stems, the conspicuous racemes, and the lack of pubescence on most parts. The collections from El Salvador differ from ours in having slightly puberulent inflorescences and resembling *Roupala montana*. There are no collections from Honduras or Nica-

ragua. The white flowers are very fragrant in anthesis; their odor resembles that of vanilla. Common names associated with these plants in Costa Rica are *Danto hediondo* and *Lora malodora*. The latter name refers to the bad odor of the cut bark. This tree was common in the forests around Zarcero; the westernmost collection in Costa Rica comes from near Monteverde, Guanacaste.

***Roupala loranthoides* Meisner, in DC., Prodr. 14:425. 1856. Figure 2.**

Probably small trees, the branchlets thick with many short twigs and clustered leaves, twigs at first reddish brown tomentulose. Leaves alternate or subopposite, pinnate leaves not seen, petioles 6–15 mm long, 1.2–2.2 mm thick, glabrous except for the very base in the leaf axil (adaxially); laminae (3) 4–7 cm long, 1.4–4.5 cm broad, broadly elliptic or oval to slightly obovate, bluntly obtuse to rounded at the apex and often emarginate, abruptly rounded or narrowed near the base and attenuate to form short wings on the petiole, margin entire in the few leaves seen and the edge revolute, drying very stiffly coriaceous, smooth and glabrous on both sides, the 3–5 pairs of major secondary veins arising at angles of ca. 20–30 degrees, both the secondary and tertiary veins slightly impressed above, venation obscure beneath. Inflorescence 5–8 cm long, axillary, exceeding the terminal leaves, racemose, glabrous, the flowers borne on thick (1–1.8 mm) pedicels, perianth ca. 8–10 mm long, less than 1 mm thick in the lower half and ca. 1.5 mm thick near the apex (dry) before anthesis, the hypogynous scales thin and triangular, very short, stigma subclavate and obtuse, thicker than the style. Fruit unknown.

A very poorly known species. Type material was destroyed by fire in Vienna, and only two small leaves and photograph remain (F). The original Friedrichsthal collection was only labeled Monte Rincon, which may be Volcan Rincon de la Vieja, Guanacaste, of northwestern Costa Rica. The thick small clustered leaves on short thick twigs suggest that this is a tree of wind gaps or exposed elfin forest.

***Roupala montana* Aublet, Pl. Guyan. Franc. 1:83. 1775. *R. complicata* H.B.K., Nov. Gen. & Sp. 2:153, t. 119. 1817. *R. borealis* Hemsl., Biol. Centr. Am. Bot. 3:78, t. 76. 1882. *R. panamensis* Pittier, Contr. U.S. Natl. Herb. 18:229. 1917. Figure 2.**

Shrubs or small trees 2–8 (rarely 18) m tall, leafy internodes 1–30 mm long, 1–6 mm thick, minutely reddish brown strigulose but quickly becoming glabrescent, becoming grayish, the axillary buds densely brownish strigulose. Leaves alternate or subopposite, heteromorphic, simple on the flowering branches, juvenile leaves pinnately compound but very variable in the number of leaflets and usually coarsely serrate, adult (simple) leaves with petioles 1.5–6 cm long, 0.7–2.5 mm thick, minutely puberulent near the base adaxially; simple leaves with laminae 4–14 cm long, 2–7.5 (9) cm broad, narrowly to broadly ovate, gradually or abruptly narrowed to the often long-acuminate apex, abruptly narrowed at the obtuse or rounded base, decurrent and forming small winged margins on the petiole, margins entire or undulate, rarely coarsely serrate as on the juvenile foliage, the laminae drying coriaceous, smooth and glabrous (in ours), often lustrous above, the 3–6 pairs of major secondary veins arising at angles of 20–50 degrees, secondary and tertiary veins slightly raised on both surfaces (dry). Inflorescences usually axillary, solitary, 7–15 (18) cm long, racemose with more than 40 flowers, rachis densely puberulent with ascending yellowish hairs 0.2–0.3 mm long, pedicel becoming 4–5 mm long densely strigulose; perianth parts 7–9 mm long, 1 mm broad, linear-oblanceolate, puberulent near the base, anthers 2–3 mm long on filaments ca. 0.5 mm long, hypogynous glands thick, ca. 0.5 mm tall, pistil ca. 6 mm long, ovary 1–1.5 mm long and densely strigose. Fruit 3–4 cm long, ca. 1.3 cm broad, asymmetrically obovate or elliptic and somewhat flattened, the surface glabrous and often lustrous, opening distally and along 1 side; seeds winged, thin and flat, ca. 2.4 cm long and 1.2 cm broad.

Trees and shrubs of the seasonally very dry deciduous and seasonally dry partly deciduous (tropical and premontane dry and moist) forest formations of the Pacific slope between 40 and 1,200 m elevations, flowering from January to March

and fruiting from June to October in Costa Rica. The species ranges from Veracruz, Mexico, to Peru, Bolivia, and Brazil.

*Roupala montana* is recognized by the stiff leaves that dry grayish and are pinately compound on juvenile shoots, but simple and long-petiolate on flowering stems, and the long puberulent racemes. Sleumer recognized both the typical form of this species and var. *dentata* (R. Br.) Sleumer as occurring in Costa Rica, but the differences between these appear to be inconsequential.

## OLACACEAE

Trees, shrubs, or woody climbers, bisexual (in ours), autotrophic or hemiparasites on roots of the host, stems with or without spines, mostly glabrous; stipules absent. Leaves alternate in a spiral or distichous (rarely opposite), simple, petioles often with ridges continuous with the laminae margins; laminae usually entire and glabrous, venation pinnate. Inflorescences 1 to several or fasciculate in the leaf axils, paniculate, racemose, cymose, or umbellate in form, often few-flowered and the flowers sometimes in groups of 3, bracteoles present or absent. Flowers bisexual, or rarely unisexual, radially symmetrical, sometimes polymorphic, often small and inconspicuous (not so in *Ximenia*, *Chaunochiton*, et al.); calyx united and usually a shallow cup with 3–6 small lobes or teeth, free or united to the ovary (as in *Schoepfia*), corolla of 3–6 petals, valvate in bud, free or united, sometimes puberulent on the inner surface; stamens as many as or 2–3 × as many as the petals, opposite the petals or petal lobes when of the same number, filaments free or adnate to the corolla tube, anthers 2-theous with mostly lateral dehiscence; a disk said to be present at the base of the ovary but usually obscure in ours, ovary superior or half-inferior (in ours), 1–5 locular (at least at the base) with the partitions often failing to reach the upper part of the ovary, ovule 1 in each locule, pendulous from the apex of the central placenta, style 1 or none, stigma 1- to 5-lobed. Fruit usually a drupe with fleshy exocarp and single seed, with endosperm, in some genera the calyx enlarges to form a colorful structure subtending the fruit.

The Olacaceae are a pantropical family with about 27 genera and 230 species. The family exhibits some interesting South American-African relationships. The Olacaceae are characterized by the woody habit, simple alternate leaves usually articulate at the base, a general absence of pubescence on vegetative parts (but not in *Minquartia*), regular flowers with very small calyx and valvate petals or petal lobes, and pistil with single style and the unusual arrangement of locules. Some genera are known to be root parasites, while others appear to be normal autotrophs; all have green leaves and resemble nonparasitic trees and shrubs. This family is very closely related to the Opiliaceae, and some authors unite the two. These families are, in turn, related to the Loranthaceae (in a wide sense) and Santalaceae (not recorded for Central America). Together, they make up the very natural order Santalales. This is a unique and rather isolated order of dicotyledons, many of which show tendencies or adaptations for parasitism and reduction of ovule structure. They share many vegetative and reproductive features, such as simple articulate entire leaves, absence of stipules, scarcity of pubescence, flowers often in triads, valvate perianth parts, poorly differentiated calyx, and pistil with an undivided style. Members of the Olacaceae may be confused with plants of the Rhamnaceae, Celastraceae, and Opiliaceae.

- 1a Young stems and inflorescences with minute branched hairs; leaves with subparallel tertiary veins; calyx not becoming expanded in fruit; corolla tube campanulate and ca. 2 mm long; tall trees of evergreen wet forests ..... *Minquartia*
- 1b Young vegetative parts and inflorescences essentially glabrous, hairs unbranched where present; leaves lacking consistently subparallel tertiary venation ..... 2a
- 2a Stems often with short thick spines, leaves often clustered on short shoots; petals free



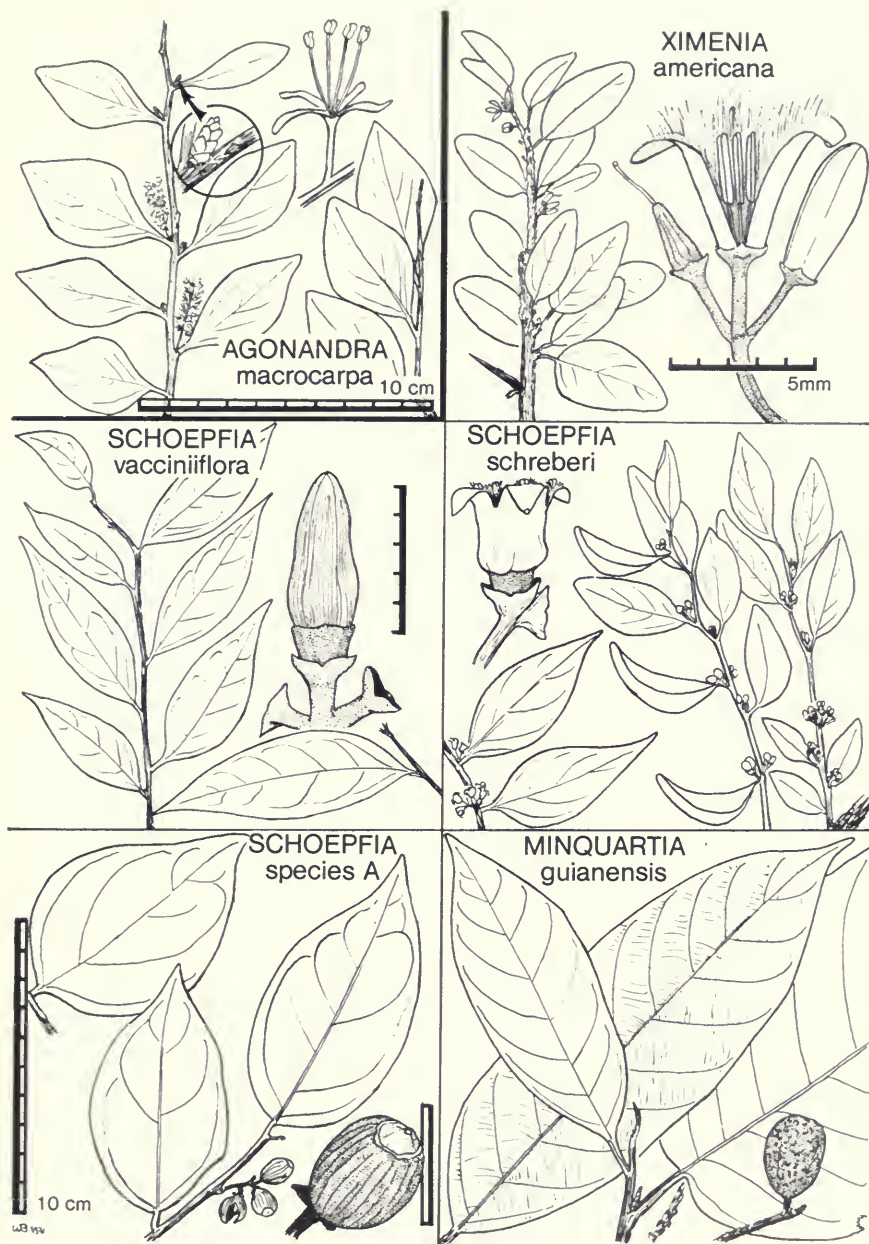


FIG. 3. Olacaceae: *Minquartia*, *Schoepfia*, and *Ximenia* species. Opiliaceae: *Agonandra macrocarpa*, upper left.

- and with conspicuous hairs within; calyx remaining small in fruit; shrubs and small trees flowering in the dry season in the Pacific lowlands. . . . . *Ximenia*
- 2b Stems lacking spines, leaves rarely borne on short shoots. . . . . 3a
- 3a Calyx very small and becoming almost completely united to the fruit, forming much of the smooth covering of the fruit and defining a small round distal area at the tip; petals united to form a short tube; shrubs to large trees in wet and dry areas *Schoepfia*
- 3b Calyx becoming enlarged in fruit and separate from the fruit, a fleshy disk or thin and broadly rotate structure. . . . . 4a
- 4a Common understory shrubs and small trees to 8 m tall; the fruit subtended by a fleshy red disk (the calyx); flowers very small and fasciculate, petals separate and 1–2 mm long, glabrous . . . . . *Heisteria*
- 4b Rare trees 10–30 m tall; fruit subtended and partly enclosed in a thin papery calyx 5–10 cm broad; flowers 1–3 cm long, petals united in the lower half and puberulent within. . . . . *Chaunochiton*

### CHAUNOCHITON Bentham

Medium-sized to large trees, bisexual, stems glabrous, lacking spines; stipules absent. Leaves simple and alternate, articulate at the base, petiolate; laminae elliptic and entire, pinnately veined, glabrous. Inflorescences of congested cymes forming small panicles in the axils of leaves. Flowers bisexual, radially symmetrical 2–6 cm long but only 2–5 mm in diameter; calyx small and cuplike, 5-toothed, becoming greatly enlarged and thin in fruit; petals 5, very narrowly linear-spatulate, valvate in bud, united in the lower half to form a narrow tube, pilose within for almost their entire length, a disk absent; stamens 5, opposite the petals and united to their base, filaments long and slender, anthers very small and clavate; ovary superior, free or united with the calyx only near the base, 2-locular with 1 pendulous ovule in each locule, style very long with globose or 5-lobed stigma. Fruit a drupe united at the base to the thin broadly expanded calyx, the calyx broadly campanulate to rotate and chartaceous, exocarp fleshy with a crustaceous endocarp.

*Chaunochiton* is a very poorly known genus ranging from Costa Rica to the Amazonian Basin. The genus is readily recognized in fruit with an expanded rotate papery thin calyx that may be 10 cm broad. The slender flowers resemble those of *Psittacanthus* (Loranthaceae), but the long narrow petals are united near the base and are puberulent within.

***Chaunochiton kappleri*** (Sagot ex Engler) Ducke, Arch. Jard. Bot. Rio de Janeiro 3:41. 1922. *Heisteria kappleri* Sagot ex Engler, in Martius, Fl. Brasil. 12, pt. 2:14. 1872. Figure 4.

Medium-sized to tall trees 12–30 m high, bisexual, leafy internodes 0.5–4 cm long, 1–4 mm thick, ashy gray in color, glabrous. Leaves alternate in a spiral, articulate at the base, petioles 6–12 mm long, with lateral ridges continuous with the lamina margins; laminae ca. 3–6 cm long and 2–3.5 cm broad, ovate-elliptic to ovate-oblong or broadly elliptic, obtuse or bluntly acute at the apex, obtuse or rounded at the base, decurrent on the petiole, margin entire, the laminae drying thin-chartaceous, smooth and glabrous above and below, with 4–7 pairs of major secondary veins, the lower secondaries often more strongly ascending than the upper. Inflorescences not seen. Flowers not seen, but if *C. breviflorum* Ducke is synonymous with this species, then the calyx should be ca. 1 mm long and the corolla ca. 1 cm long with the petals ca. 0.5 mm broad at the base and 1 mm broad at the thickened apex. Fruit a drupe 6–10 mm long and 5–10 mm in diameter, with a somewhat muricate surface when dry, the fruit is subtended by the expanded calyx which may be 8–12 cm broad, subentire or weakly 5-lobed, drying pale brown and membranaceous, apparently rotate or slightly campanulate in form, the fruiting pedicel 15–20 mm long.

Plants of lowland evergreen wet forest formations and known from only a single collection in North America. Fruit and leafless stems were collected by Pittier

(11948) in the Diquis basin at ca. 600 m altitude on March 15th, 1898. The species is otherwise only known from Amazonian Brazil and the Guianas.

*Chaunochiton kappleri* is recognized by the fruit being subtended by a thin broad calycular development and the slender flowers with the petals puberulent within. The small leaves clearly articulate at the base, lack of pubescence, weakly five-lobed calyx, and small ovary are all characteristic of Olacaceae. The collection from Costa Rica is said to have been a small slender tree 12–15 m high and 20–25 cm diameter. Its local name is said to be *Manglillo*. Botanists visiting the General Valley, Osa Peninsula, and Golfo Dulce region should keep this unusual plant in mind; the species and the genus are very poorly known.

### HEISTERIA Jacquin

Shrubs or small trees, rarely woody lianas as in *H. scandens*, not known to be parasitic, bisexual, the young stems with longitudinal ridges, glabrous. Leaves alternate and often distichous, articulate at the base, petioles usually with 2 adaxial ridges continuous with the lamina margins; lamina entire, glabrous, with laticiferous ducts. Inflorescences of few to many flowers in axillary fascicles, often forming a raised mound of tissue with sessile scarious bracts irregularly arranged over the surface. Flowers bisexual, very small, pale green to white or yellowish, pedicellate to subsessile, glabrous on the outside, calyx usually broadly cup-shaped, subtentire to 5- or 6-toothed or -lobed, free from the ovary, becoming enlarged and thickened in fruit; petals usually 5 (6), valvate in bud, free or united at the very base, glabrous or puberulent within; stamens 10 or 12 (rarely 5 or 6), free or united to the base of the petals, antipetalous stamens often shorter than the antisepalous, anthers rounded and minute; ovary superior, rounded to conical, with 3 locules in the lower half, 1 pendulous ovule in each locule, style short or none and with 3 poorly differentiated stigmas. Fruit a drupe with thin fleshy exocarp that is often black and borne on the expanded brightly colored calyx, the fruiting calyx annular, broadly cupulate or becoming reflexed, fleshy in texture and red to purple in color, the embryo small in the top of the endosperm.

The genus, with probably fewer than 20 species, ranges from southern Mexico and the Lesser Antilles to southern Brazil and Bolivia. Two species are native to West and Central Africa. Species of *Heisteria* are easily recognized in fruit because of the expanded, slightly fleshy calyx. The usually black fruit and bright red calyx produce a striking contrast, undoubtedly an adaptation for seed dispersal. The very small flowers arising directly from an axillary base are difficult to see and rare in collections. The American species are seriously in need of revision, and our own species represent some difficult unresolved problems. This is particularly true regarding *H. acuminata*, *H. macrophylla*, and *H. costaricensis*. A number of collections appear to be intermediate between these taxa, and all three may prove to be part of a polymorphic complex. All our species appear to be plants of the forest shade.

- 1a Woody lianas (perhaps beginning as shrubs); laminae occasionally with the lowest pair of secondary veins quite prominent and almost triplinerved; petals puberulent within; fruit red at maturity and subtended by a small (10–15 mm) calyx; 0–800 m elevation ..... *H. scandens*
- 1b Shrubs or trees; laminae never with the basal pair of secondary veins very prominent; fruiting calyx often more than 12 mm broad ..... 2a
- 2a Petals puberulent within; fruit white at maturity, fruiting calyx conspicuously and deeply 5-lobed; leaves lustrous above and subcoriaceous when dry with the margins recurved, short-acuminate at the apex; 0–800 m elevation ..... *H. concinna*
- 2b Petals glabrous within; fruit becoming black in late stages, fruiting calyx shallowly or obscurely 5-lobed; leaves not usually lustrous or with the margins recurved when dry, chartaceous ..... 3a

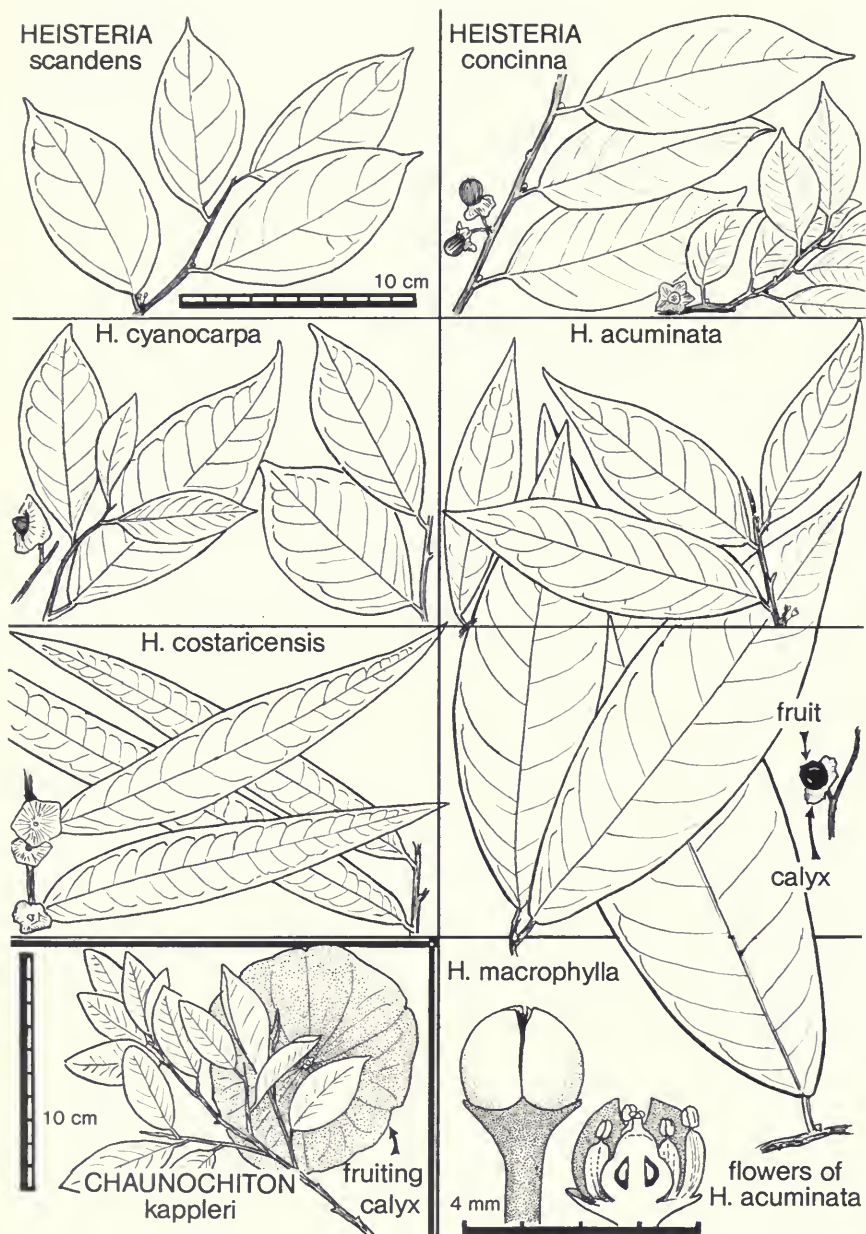


FIG. 4. Olacaceae: Costa Rican species of *Heisteria* and *Chaunochiton*.



- 3a Laminae usually abruptly narrowed at both ends; petiole deeply and narrowly canaliculate above (adaxially); fruit becoming black only in late stages, the fruiting calyx often reflexed; 0–300 m elevation ..... *H. cyanocarpa*
- 3b Laminae usually gradually narrowed to the apex; petiole with the adaxial ridges forming a V-shaped or broadly U-shaped sulcus above, rarely narrowly canaliculate above; 0–1,700 m elevation. (Note: The following 3 species are differentiated here on the bases of leaf form and habitat. Plants with intermediate characteristics are not uncommon, and it may be that these 3 taxa are part of a single polymorphic complex.)..... 4a
- 4a Laminae linear-lanceolate, widest below the middle and often narrowed abruptly at the base; 0–700 m elevation ..... *H. costaricensis*
- 4b Laminae not linear-lanceolate ..... 5a
- 5a Plants rarely found below 500 m elevation; laminae rarely more than 15 cm long, not usually tapering gradually to both base and apex, often drying pale in color; understory plants of montane and seasonally dry evergreen moist forest formations; fruit ellipsoid-oblong. .... *H. acuminata*
- 5b Plants rarely found above 500 m elevation; laminae usually more than 15 cm long, often tapering gradually to both base and apex, drying dark in color; plants of wet forest formations; fruit globose ..... *H. macrophylla*

***Heisteria acuminata*** (H. & B.) Engler, in Martius, Fl. Brasil. 12(2):14, nota. 1872; and in Flora 56:135. 1873. *Rhaptostylum acuminatum* Humboldt and Bonpland, Plant. Aequinox. 2:129, 5:125, 1809, and in H.B.K., Nov. Gen. & Sp. Pl. 5, t. 621, emended illustration. 1824. Figure 4.

Shrubs or small treelets 0.7–3 m tall, glabrous, the leafy internodes 0.3–4 cm long, 1–4 mm thick, with 2 or 4 distinct longitudinal ridges, becoming terete and often drying pale in color. Leaves obscurely articulate at the base, petioles 4–8 (11) mm long, the 2 longitudinal adaxial ridges separate or forming a V-shaped sulcus above; laminae 6–14 (23) cm long, 2–5 (7) cm broad, elliptic to very narrowly elliptic or elliptic-oblong (rarely lanceolate or ovate elliptic), usually widest near the middle, tapering gradually to the short- or long-acuminate apex, obtuse to acute at the base, margin entire or undulate when dry, the laminae drying thin- to stiff-chartaceous, glabrous and smooth above and below, the 5–10 pairs of major secondary veins usually quite distinct from the tertiary veins. Inflorescences in the axils of leaves, or less often in the axils of fallen leaves and undeveloped leaves, usually with only 1 or 2 flowers in anthesis at a node at one time, pedicels 2–4 mm long; flowers 2–3 mm long, calyx prominently 5-toothed, 1.5–2 mm broad, petals ca. 2 mm long and 1 mm broad, glabrous within; stamens 10 and clearly of 2 lengths with the longer alternipetalous, filaments to 0.4 mm broad, anthers 0.2–0.3 mm broad, pistil ca. 1.2 mm long and 1 mm broad at the base. Fruit ca. 8–10 mm long and 6–8 mm in diameter, globose to ellipsoid, soon becoming black, longitudinally ribbed when dry, the fruiting calyx 12–20 (30) mm broad, inconspicuously 5-lobed, bright red, fruiting pedicels ca. 7 mm long.

Plants of forest understory in moist evergreen montane or, less often, lowland formations; collected with fruit from October to April, but probably flowering throughout the year. The plants are most often encountered between 600 and 1,600 m elevation in Costa Rica. The species ranges from Chiapas, Mexico, to Colombia (see below).

*Heisteria acuminata* is recognized by its small- to medium-sized, usually elliptic leaves that taper gradually to an acuminate apex, glabrous flowers, weakly lobed fruiting calyx that is broader than the fruit, and its frequent occurrence in cloud forests on the Pacific slope. These plants are not known from below 600 m on the Pacific slope of Costa Rica and adjacent Panama. The few lowland collections of the Caribbean slope appear to be restricted to the moist (not the wet) forest formations as diagrammed by Tosi in the Mapa Ecológico. Our highland material is very similar to that of Guatemala and Chiapas, but I have seen no comparable highland material from Colombia. Much of the Central American material has been referred to as *H. macrophylla* or misidentified as *H. longipes* in the past.

The original collection of *Heisteria acuminata* is from Popayan, Colombia, at about 2,000 m elevation. The leaf shape and venation and floral details illustrated for this species agree well with Central American highland material. In a recent letter, Dr. Sleumer points out that the fruit of *H. acuminata* is larger and ellipsoid-oblong, whereas the fruit of *H. macrophylla* is smaller and globose. He thus interprets the species in a way that has *H. acuminata* reaching its northern limit in Costa Rica, whereas *H. macrocarpa* reaches its southern limit in Costa Rica. This species may also intergrade with *H. costaricensis*, and it is closely related to *H. cyanocarpa*: see the discussions under those species and *H. macrophylla*.

***Heisteria concinna*** Standley, Publ. Field Columbian Mus., Bot. Ser. 8:137. 1930. Figure 4.

Small- to medium-sized trees 3–10 (20) m tall, the branches often said to be drooping, leafy internodes (0.5) 1–4 (7) cm long, 1–3 (4) mm thick, yellowish or pale brown with 2 often obscure longitudinal ridges, becoming minutely striate and yellowish or pale brown when dry, glabrous. Leaves distichous, often clearly articulate only in age, petioles 7–20 mm long, 1–2 mm thick, often bent distally and thickened beneath, the adaxial petiolar ridges usually forming a narrow (0.5 mm) sulcus above; laminae (3) 5–15 cm long, 2.5–6 (7) cm broad, elliptic to broadly elliptic to ovate-elliptic, tapering gradually or abruptly to the acuminate apex, obtuse or somewhat rounded at the base, margins entire but becoming undulate and recurved when dry, the laminae drying subcoriaceous or very stiffly chartaceous and lustrous above, smooth on both surfaces, the 5–8 pairs of major secondary veins often difficult to distinguish from the tertiary venation. Inflorescences in the axils of current or fallen leaves, pedicels 3–6 mm long; flowers white, flower buds ca. 2–3 mm long before anthesis, calyx ca. 1 mm high and 2–3 mm broad, petals ca. 2 mm long, puberulent within, anthers 0.2–0.3 mm long, ovary conical, 1.5 mm long. Fruit 10–14 mm long and 8–10 mm thick (dry), ellipsoid to globose, becoming white, fruiting calyx 2–4 cm in diameter with usually 5 shallow or relatively pronounced rounded lobes, rose red to dark red in color.

This species is found in moist (partly deciduous) and wet evergreen forest formations between sea level and about 800 m elevation on both the Caribbean and Pacific slopes in Costa Rica; fruiting collections have been made from September through March. The species probably ranges from the Caribbean side of Honduras (*Standley 55292*) to eastern Panama.

*Heisteria concinna* is distinguished by its stiff lustrous leaves with unusual petioles, puberulent petals, and the mature white fruit subtended by a bright red five-lobed calyx that is 2 to 4 cm broad. Most of our collections come from seasonally dry evergreen forests on the Pacific slopes, but none come from the seasonally very dry and largely deciduous formations of lowland Guanacaste. This species is apparently very closely related to *H. coccinea* Jacquin of the Lesser Antilles.

***Heisteria costaricensis*** Donnell Smith, Bot. Gaz. 19:254. 1894. Figure 4.

Shrubs or slender treelets 1.5–2.5 (3) m tall, leafy internodes 0.3–4 cm long, 0.7–3 (5) mm thick, with 2 or 4 longitudinal ridges 0.1–0.3 mm high, the stems becoming smooth and terete. Leaves alternate and distichous, indistinctly articulate at the base, petioles 4–8 (13) mm long, the longitudinal adaxial ridges usually forming a shallow groove ca. 1 mm wide above, the petiole occasionally thickened and bent; laminae 12–22 (30) cm long, 1.5–3.5 (4.5) cm broad, narrowly lanceolate to linear-lanceolate, broadest below the middle (rarely near the middle), tapering very gradually to the acute or acuminate apex, narrowed more abruptly to the acute or slightly rounded base, margin entire or slightly undulate, the laminae drying chartaceous to stiffly chartaceous, smooth on both surfaces, the 7–37 pairs of major secondary veins usually easy to distinguish from the tertiary. Inflorescences small

axillary fascicles with apparently only a few flowers at any one time; flower buds ca. 1.5 mm long and subglobose, mature flower with 5-toothed calyx, petals ca. 2 mm long and 1 mm broad, glabrous on both surfaces; stamens 10, filaments liguliform, anthers 0.2–0.3 mm long; pistil conical, ca. 1 mm long and 1 mm in diameter. Fruit globose or ovoid 6–8 mm long, becoming black, vertically ribbed when dry, fruiting calyx 12–25 mm broad, obscurely or shallowly 5-lobed, bright red, the fruiting pedicels 3–9 mm long.

Plants of wet and moist evergreen forest formations on both the Caribbean and Pacific slopes from sea level to 700 (1,000) m elevation, but not as yet collected from below 500 m on the Caribbean side; probably flowering and fruiting throughout the year. This species is known only from Costa Rica and Panama.

*Heisteria costaricensis* is immediately recognized by its long linear-lanceolate leaves, widest below the middle and usually abruptly narrowed near the base. Characters of flower and fruit are probably the same as those of *H. acuminata* and *H. macrophylla*. These three species are separated here primarily on their different leaf shape, but they may prove to be members of a single polymorphic species. Collections from around San Ramon, Alajuela, appear to be intermediate between typical *H. acuminata* and *H. costaricensis*.

***Heisteria cyanocarpa*** Poeppig, Nov. Gen. Sp. 3:35, t. 241, 1845 (fide Sleumer in herb.). *H. longipes* Standley, J. Wash. Acad. Sci. 17:8. 1927. Figure 4.

Shrubs or small- to medium-sized trees (1.5) 3–12 (20) m tall, leafy internodes 0.5–3 cm long, 1–3 mm thick, with 2 or 4 longitudinal ridges, becoming terete, glabrous. Leaves alternate, usually distichous, articulate at the base, petioles 4–12 mm long, 1–1.5 mm thick, the 2 adaxial longitudinal ridges forming a very narrow sulcus above, becoming longitudinally striate and thickened abaxially throughout the length of the petiole; laminae (4) 6–14 cm long, 2–6 (7) cm broad, elliptic to ovate-elliptic, obovate, or oblong, gradually or abruptly narrowed to the short acuminate apex, abruptly narrowed at the obtuse (rarely acute) base, margin entire or undulate when dry, laminae drying stiffly chartaceous, smooth on both surfaces, with 5–9 pairs of major secondary veins but the secondaries often difficult to distinguish from the tertiaries. Inflorescences in the axils of current or recently fallen leaves, with 5–10 flowers but only 1 or 2 flowering at a node at one time, flower buds 1.5–2 mm long, pedicels 1–4 mm long; flowers with a 5-lobed calyx, petals 1.5–2 mm long, glabrous within; anthers 10, borne at the edge of the disk, filament ca. 1.2 mm long and 0.5 mm broad, narrowed below the minute (0.2 mm) anther, ovary 1–1.3 mm broad near the base, ca. 1.2 mm long, abruptly narrowed above, stigma obscurely lobed. Fruit 8–12 mm long, 6–8 mm in diameter, ellipsoid, apparently remaining green for a time but becoming black, fruiting calyx (1) 1.5–2 (2.5) cm broad, bright red, often reflexed, usually bluntly 5-lobed.

Plants of evergreen and partly deciduous wet and moist forest formations from sea level to about 300 m elevation on both the Caribbean and Pacific slopes; flowering collections have been made from December through July, and fruiting collections have been made from January to September. The species, as presently understood, ranges from southwestern Costa Rica and the Bocas del Toro region of Panama to Colombia.

*Heisteria cyanocarpa* is recognized by the laminae usually being abruptly narrowed at both ends, the petiole narrowly canaliculate above, and the five-lobed fruiting calyx subtending a green fruit that becomes black only at maturity. The species appears to be restricted to the lowlands (below 300 m) in our area, but collections from Colombia which appear to be this species come from as high as 1,500 m. Rather similar looking plants from above 500 m elevation on the Pacific slope and along the Caribbean slope are here placed under *H. acuminata*. In a recent letter (June 1980), Dr. Sleumer suggests that this species might be made part of *H. acuminata* in a very wide sense.



***Heisteria macrophylla*** Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjoebenhavn 1856:40. 1857, sensu stricto. *H. latifolia* Standley, J. Wash. Acad. Sci. 17:8. 1927.

Shrubs or small treelets (0.5) 1.5–3 (7) m tall, glabrous, the leafy internodes 0.3–6 cm long, 1–5 mm thick, with 2 or 4 distinct longitudinal ridges, becoming terete in age, often drying pale in color. Leaves obscurely articulate at the base, petioles 3–18 mm long, ca. 3 mm thick, the 2 adaxial longitudinal ridges separate or forming a broad V-shaped sulcus above; laminae 15–36 cm long, 5–10 (17) cm broad, very narrowly elliptic to broadly elliptic or ovate-elliptic, tapering very gradually to the long-acuminate apex, tapering gradually to the acute or obtuse base, occasionally slightly rounded at the petiole in larger laminae, margin entire (undulate when dry), the laminae drying thin-chartaceous and often dark in color, glabrous and smooth on both surfaces, the 9–17 pairs of major secondary veins usually quite distinct from the tertiary veins. Inflorescences in the axils of leaves or fallen leaves, pedicels 1–3 mm long; flowers 2–3 mm long, calyx 5- (rarely 6-) toothed, petals 5 (rarely 4), ca. 2 mm long and 1 mm broad, glabrous; stamens 10, filaments ca. 0.5 mm broad, 0.7–1.5 mm long, anthers ca. 0.5 mm broad, pistil conical ca. 1 mm broad at the base. Fruit ca. 8–10 mm long and 6–9 mm in diameter, globose to ovoid or ellipsoid, soon becoming black, longitudinally ribbed when dry, the fruiting calyx 16–30 mm broad, inconspicuously 5-lobed, bright red, the fruiting pedicel ca. 7 mm long.

Plants of the wet evergreen forest formations of the Caribbean lowlands and adjacent slopes between sea level and about 300 m elevation; fruiting collections have been made from August to October and January to May. The species, as here delimited, ranges from southern Nicaragua to eastern Panama.

*Heisteria macrophylla* (in a narrow sense) is recognized by its larger leaves usually widest near the middle and gradually tapering to both apex and base and the wet forest habitat on the Caribbean slope. The large thin leaves are often rhombic in outline. There are collections (Molina *et al.* 17339, Pittier & Tonduz 9174, Donnell Smith 6462, and Standley 37331) which appear to be intermediate between typical *H. macrophylla* and *H. acuminata*. Further study may show that *H. macrophylla* is only an unusual lowland form of *H. acuminata* in a wide sense (q.v.); see Figure 4.

***Heisteria scandens*** Ducke, Arch. Jard. Bot. Rio de Janeiro 4:9. 1925. *H. fatoensis* Standl., Publ. Field Columbian Mus., Bot. Ser. 8:137. 1930. *H. eurycarpa* Standl., loc. cit. 11:148. 1936. Figure 4.

Woody lianas climbing to the tops of trees as much as 30 m tall, perhaps beginning as small shrubs 3–4 m tall, leafy internodes 0.6–4 (6) cm long, 0.7–2.5 (5) mm thick, the 2 longitudinal ridges absent or inconspicuous, the stems soon becoming terete, longitudinally minutely striate and pale gray to dark brown when dry, the axillary cushion-like inflorescence bases often conspicuous on the leafless stems. Leaves usually distichous with the laminae in a single plane, articulate at the base, glabrous, petioles 5–12 (20) mm long, 0.6–1.3 mm thick, the 2 adaxial ridges forming a shallow groove above; laminae (4) 5–13 cm long, (1.5) 3–6 cm broad, ovate-oblong to elliptic-oblong or broadly elliptic, abruptly narrowed to the short (0.5–1 cm) acuminate apex, obtuse to abruptly rounded at the base, margin entire or slightly undulate, the laminae drying thin chartaceous or chartaceous, smooth on both surfaces and often somewhat lustrous above, venation with 3–5 pairs of major secondary veins, occasionally with the lowest pair of veins quite prominent and the lamina almost triplinerved. Flowers fasciculate from a broad minutely bracteate mound in the axils of leaves or fallen leaves, each axil producing up to 30 (50) flowers but only a few seen in anthesis in our material, pedicels 3–6 mm long, ca. 0.3 mm thick, flowers 2–3 mm long, glabrous on the outside, calyx 1–2 mm broad, with 5 short (0.5 mm) teeth, petals 1.5–2 mm long, minutely puberulent near the apex within; stamens 10, filaments 1–1.5 mm long, anthers 0.2–0.3 mm long; ovary conical and ca. 1 mm broad at the base, with shallow longitudinal sulci. Fruit 9–14 mm long, 8–12 mm in diameter, globose to ellipsoid, becoming red at maturity and longitudinally ribbed when dry, fruit-



ing pedicel ca. 1 cm long, fruiting calyx 10–15 mm broad with 5 shallow lobes, the calyx smaller than the fruit and often reflexed.

This species is known from only two collections in Costa Rica, both from the Golfo Dulce region: *Allen 5838* at 75 m altitude and *Lent 447* at about 650 m. Fruit have been collected in February and March and in July and August in Costa Rica and Panama. The species, as presently known, ranges from the Golfo Dulce area of Costa Rica (on the Pacific side) and the province of Bocas del Toro in Panama (on the Caribbean side) southward to Peru and Amazonian Brazil.

*Heisteria scandens* is immediately distinguished by its climbing habit, apparently unique in the genus. The smooth terete branches with well-spaced leaves, unusual leaf venation, petals puberulent within, and the fruit apparently red at maturity with relatively small fruiting calyx further distinguish these plants. This species may be closely related to *H. acuta* Engler of Brazil.

### MINQUARTIA Aublet

Trees, often large, apparently autotrophic, bisexual, the young branches rusty tomentulous with branched hairs, the older stems sometimes perforated, lacking spines. Leaves alternate, not clearly articulate at the base, petiolate; laminae elliptic and acuminate, entire, chartaceous to coriaceous, glabrous above but minutely puberulent beneath, with resin canals and lactiferous ducts. Inflorescences spicate, solitary in the leaf axils, puberulent, with small bracts subtending the subsessile or short-pedunculate cymelike groups of flowers; flowers bisexual, calyx cuplike and 5-toothed, persistent but not enlarging in fruit, petals connate into a bell-shaped or campanulate tube, puberulent to villous within, the 5 (6) lobes valvate in bud; stamens 10 (12) in 2 whorls, adnate to the lower part of the corolla tube at 2 levels, sessile or on short filaments, the antepetalous anthers longer than the antesepalous; ovary with 3–5 locules, stigma 3- to 5-lobed. Fruit with a somewhat fleshy exocarp and crustaceous endocarp.

A genus of perhaps three species, ranging from southern Central America to the Amazonian Basin. The genus stands out among our representatives of the family because of the unusual pubescence. Plants with immature inflorescences may be mistaken for species of Euphorbiaceae or Malvales.

***Minquartia guianensis* Aublet, Hist. Pl. Guyan. Franc., Suppl. 4, t. 370. 1775.**  
Figure 3.

Trees 10–35 m tall, developing low buttresses, sapwood yellow with dark red or dark brown heartwood, bisexual, leafy internodes 0.7–3 cm long, 1.4–3 mm thick, at first slightly angled but soon becoming terete, very minutely (0.05 mm) brownish puberulent but soon becoming glabrous, smooth and brownish; stipules none but the young folded leaves stipule-like, often ca. 1 cm long and 1.5 mm thick and tapering to a narrow apex. Leaves alternate and distichous, petioles 8–30 mm long, 1–2.8 mm thick, with 2 longitudinal adaxial ridges continuous with the margins of the lamina, the ridges expanded and slightly vaginate just below the apex of the petiole; laminae 8–16 (22) cm long, 3–7 (11) cm broad, elliptic-oblong to ovate-oblong, abruptly short (1–2 cm) acuminate at the base, margin entire but often slightly undulate, drying chartaceous and slightly lustrous above, smooth and glabrous above and below, venation pinnate with 3–14 pairs of major secondary veins, arcuate ascending only near the margin and never loop-connected, tertiary venation often subparallel between the secondaries. Inflorescence solitary in the leaf axils, spikelike with alternate groups of usually 3 flowers subtended by a bract, rachis with a covering of minute scurfy or branched reddish brown hairs, ca. 5 cm long at anthesis and to 15 cm long in fruit. Flowers apparently bisexual, short pedicelled, calyx broadly cupulate with 5 very short teeth, ca. 1 mm long and 1.5–2 mm broad, reddish brown puberulent, corolla a campanulate tube ca. 2 mm long with 5 recurved lobes, puberulent, stamens 10, borne on the tube on very short (0.5 mm) filaments, anthers broader than long; ovary with

an unusual pubescence forming ca. 10 small pocket-like depressions on the upper (distal) sides, style with 5 distinct finger-like stigmas. Fruit becoming 3 cm long and 2 cm thick, black and fleshy, edible but with an acrid taste, borne on a short (5 mm) thick (2 mm) pedicel.

Trees of the lowland evergreen wet forest formations below 500 m elevation in Costa Rica; mature fruit have been collected in July, but mature flowers have not been collected in Central America. The species ranges from southern Nicaragua to Ecuador and Amazonian Brazil.

*Minquartia guianensis* is recognized by the tall habit, simple alternate distichous glabrous leaves with unusual petioles and subparallel tertiary venation, solitary spikelike reddish brown inflorescences, and small densely puberulent flowers. These trees are known by the names *Manu*, *Crillo*, *Nispero*, *Negro*, *Cricamola*, and "Black Manwood" in Costa Rica and Panama. The species is largely represented by sterile collections in herbaria; the flower descriptions are based on South American material. The wood is very hard and very durable, resisting both termites and fungal decay (see Biotropica 8:71-95, 1976).

### SCHOEPIA Schreber

Shrubs or trees, reported to be root parasites, bisexual, without spines, the vegetative parts glabrous; stipules none. Leaves alternate, clearly articulate at the base, petiolate, the laminae entire and stiffly chartaceous to coriaceous, glabrous, venation pinnate. Inflorescences solitary to several or fasciculate in the leaf axils, racemose or spicate with usually 3 (2-5) flowers closely clustered or short-pedicellate at the end of a short peduncle (and often resembling the triads of Loranthaceae), bract subtending the ovary of each flower a shallow usually 3-lobed cup, glabrous or puberulent. Flowers small, calyx united with the ovary and with an obscurely 3- to 6-lobed or entire distal margin, glabrous, usually green, corolla united to form a tube, the corolla lobes usually 5 (3-6), short and valvate in bud, the corolla glabrous on the outside and usually puberulent near the stamen attachment within; stamens epipetalous, high on the corolla tube, anthers sessile or subsessile, small, about as wide as long; ovary half-inferior, the upper surface often minutely puberulent, style 1 with a prominent rounded or 3-lobed stigma, base of the ovary imperfectly 3-locular, ovules 3, lacking an integument. Fruit a drupe enclosed by the smooth-walled calyx except near the apex where a circular area of different texture is demarcated by the calycular rim, seed 1 and apparently erect, embryo small at the top of the endosperm.

A genus of about 35 species in tropical Asia and ranging in the New World from Mexico through Central America and the West Indies to Bolivia and southern Brazil. The genus is distinguished by the simple stiff alternate leaves articulate at the base, short few-flowered axillary inflorescences, tubular corolla with epipetalous stamens opposite the valvate corolla lobes, half-inferior ovary with poorly differentiated adnate calyx, and unusual fruit with circular apical area of different texture than the smooth lower surface.

- 1a Trees to 20 m tall in the wet evergreen forests of the Caribbean lowlands; leaves 3-6 cm broad with strongly ascending basal secondary veins. . . . . *S. species A*
- 1b Shrubs or trees rarely more than 10 m tall in deciduous and partly deciduous forests of the Pacific slope in Costa Rica; leaves 1-4 cm broad. . . . . 2a
- 2a Corolla tube campanulate, 2-5 mm long and 2-3 mm in diameter; flowers usually sessile in groups of 3; leaves ovate to lanceolate on pale grayish white stems; 0-1,000 m altitude . . . . . *S. schreberi*
- 2b Corolla tube cylindrical, 4-7 mm long and 2-3 mm in diameter; flowers often short-pedicellate; leaves usually elliptic on brownish stems; 800-1,800 m altitude  
*S. vacciniiflora*

**Schoepfia schreberi** J. F. Gmel., Syst. Veg. 2:376. 1791. *S. americana* Willd., Sp. Pl. 1:996. 1798. *S. arborescens* Roem. & Schult., Syst. 5:160. 1819. Figure 3.

Trees 4–8 (rarely 25) m tall, without spines, leafy internodes 0.5–2.5 cm long, 0.7–3 mm thick, at first somewhat angular or ridged but soon becoming terete, becoming pale grayish white and smooth, then dark in later years. Leaves alternate and distichous, clearly articulate at the base; petiole differentiated from the lamina, ca. 4–8 mm long, with lateral ridges continuous with the lamina margins, not sulcate above; lamina 3–8 cm long, 1.5–3.5 cm broad, ovate, ovate-elliptic to narrowly elliptic or lanceolate, acute to acuminate at the apex, acute to obtuse at the base and with the margins attenuate on the petiole, margins entire and often undulate, lamina drying very stiffly chartaceous or subcoriaceous, smooth and glabrous above and below, venation pinnate with 2 or 3 (sometimes to 5) pairs of major secondary veins, the basal secondaries often strongly ascending, prominent beneath. Inflorescences fasciculate in the leaf axils, the flowers usually borne in groups of 3 (triads) on short (2–6 mm) thin (0.4 mm) glabrous peduncles, flowers sessile within broad (1.5–2 mm) shallow (0.5–1 mm) cuplike bracts with irregular and partly puberulent margins, the bracts closely approximate at the apex of the peduncle. Flowers 3–5 mm long, calyx glabrous and obscurely 5-lobed, or entire, corolla tube campanulate, 2–4 (5) mm long, 2–3 mm in diameter, the corolla lobes 1–2 mm long and recurved, glabrous on the outside but puberulent around the anther attachment within, stamens sessile high on the corolla tube, anthers ca. 0.6 mm long; top of the half-inferior ovary minutely grayish puberulent, style ca. 1 mm long with a prominent flattened disklike stigma ca. 0.5 mm broad. Fruit globose to ellipsoid, ca. 7 mm long and 6 mm in diameter, greenish (immature?) with a red apex, the glabrous lower ovary and calyculus defining a small circular distal minutely puberulent area at the top of the fruit ca. 2 mm broad and yellowish in color.

Trees of deciduous and partly deciduous forest formations on the Pacific slope of Costa Rica between sea level and 1,000 m elevation; flowering material has been collected from December to February and in June and July in Costa Rica. The species, as presently understood, ranges from southern Florida and Mexico to northern South America and the West Indies.

*Schoepfia schreberi* is recognized by its glabrous alternate stiff little leaves that are clearly articulate on pale-colored twigs, the triads or diads of flowers arising from small mounds of tissue in the axils of leaves, and the small bracteate flowers with campanulate corolla tube, epipetalous sessile anthers, and internal pubescence.

**Schoepfia vacciniiflora** Planch. ex Hemsley, Diag. Pl. Mex. 5. 1878. Figure 3.

Shrubs or small trees 2–8 (12) m tall, without spines, leafy internodes 0.3–3 cm long, 0.6–4 mm thick, strongly 2-ridged or angled in early stages but becoming terete, pale brown to pale gray. Leaves alternate and distichous, clearly articulate at the base, petioles weakly differentiated from the lamina, ca. 2–5 mm long, with lateral margins continuous with the lamina margins, flat above (adaxially); laminae (2) 3–8 (10.5) cm long, 1–3 (4.5) cm broad, elliptic to elliptic-oblong or ovate-elliptic, acute to short-acuminate at the apex, acute to obtuse at the base and somewhat attenuate at the petiole, margins entire or slightly undulate, drying stiffly chartaceous to subcoriaceous, smooth and glabrous on both surfaces, venation pinnate with 3–6 pairs of major secondary veins, the lower pairs of secondaries often strongly ascending (in ours), sometimes loop-connected near the margin. Inflorescences usually 1 or 2 in the axils of leaves, the peduncle branched above the 1st flower or the flowers subsessile and clustered at the end of the peduncle, flowers 2 to 4 per inflorescence (most often 3), the flowers usually on short pedicels with shallow cupulate bracts beneath the base, the bracts 1.5–2 mm broad, generally 3-lobed, glabrous. Flowers 6–8 mm long, calyx fused with the ovary and with an entire or obscurely 5-lobed distal margin, corolla tube (4) 5–7 mm long, 2–3 mm in diameter, cylindrical, corolla lobes 1–1.5 mm long, slightly reflexed at anthesis, glabrous on the outside, puberulent near the stamen attachment within, anthers sessile high on the corolla tube, style ca. 2 mm long with stigma 1 mm broad. Fruit ellipsoid, ca. 10 mm long and 6 mm in diameter, glabrous,

longitudinally striate when dry, glabrous except for a sharply defined circular distal area 1.5–2 mm in diameter at the apex.

Plants of the partly deciduous forest formations on the Pacific slope between 800 and 1,200 (1,800) m elevation in Costa Rica; apparently flowering from June to January. The species ranges from Guatemala to Costa Rica.

*Schoepfia vacciniiflora* is characterized by the stiff distichous leaves articulate at the base, small usually pedicellate flowers with tubular corolla, and ellipsoid fruit with circular distal area of different texture around the apex. This species is quite easily distinguished from *S. schreberi* in Guatemala where the plants differ consistently in flower form and altitudinal range. These distinctions are not so clear-cut in Costa Rica where we have very few collections that are clearly referable to *S. vacciniiflora*: Brenes 3554, 5367, 5661, 20334, 21051, all from near San Ramon, Alajuela province. Two high-altitude collections from 1,700 to 1,800 m altitude with shorter less cylindrical corolla tubes are tentatively placed here: A. Jimenez 289 and M. Valerio 1657 from San Jose province.

### **Schoepfia species A. Figure 3.**

Trees ca. 20 m tall, leafy internodes 1–3 cm long, 1.5–3 mm thick, 2-ridged in early stages, becoming terete and grayish brown. Leaves distichous, articulate at the base, petioles 3–6 mm long, with 2 adaxial ridges becoming lateral in the distal half of the petiole and continuous with the margins of the lamina, sulcate above at the base; laminae 5–11 cm long, 3–6 cm broad, ovate to ovate-oblong, acute to short-acuminate at the apex, rounded and truncate or occasionally obtuse at the base, margins entire and revolute when dry, laminae drying stiffly chartaceous, smooth and glabrous above and below, venation pinnate with 3–5 pairs of major secondary veins, the lowest 2–4 secondary veins strongly arcuate ascending. Inflorescences 1 or 2 in the axils of leaves, the peduncles becoming 6–12 mm long and bearing usually 3 subsessile or shortly pedicellate flowers distally. Flowers not known. Fruit ellipsoid, ca. 12–14 mm long and 9–12 mm in diameter, red but drying dark brown and lustrous with numerous longitudinal shallow grooves, a circular area of different texture ca. 4 mm wide delimited by the calycular rim near the apex of the fruit.

Plants of the lowland Caribbean rain forest formations. The species is known only from a single fruiting collection made in March, near the Rio Kama-Rio Escondido in Bluefields, Nicaragua, by Proctor, Jones, & Facey (26972).

*Schoepfia* species A is recognized by the stiff ovate leaves articulate at the base and with ascending basal secondary veins, the characteristic fruit on short peduncles, and the lowland Caribbean forest habitat. This species resembles *S. obliquifolia* Turcz. of Venezuela and Brazil, but without flowers it is difficult to say where its true affinity lies. The very distinctive fruit and articulate leaves leave no doubt that this tree is placed in the correct genus.

### **XIMENIA Linnaeus**

Shrubs and small trees, hemiparasitic on roots of other plants, bisexual, stems with thick spines produced by modified axillary branchlets, glabrous or puberulent. Leaves alternate, articulate at the base, often borne in fascicles from short shoots, deciduous; laminae ovate to elliptic, entire, pinnately veined. Inflorescences axillary, 1 to several and fasciculate, usually a few- to many-flowered bracteate cyme or umbel, flowers sometimes solitary. Flowers bisexual, regular, hypogynous, medium-sized, whitish; calyx small with 4 or 5 small teeth or lobes, not expanding in fruit; corolla of 4 or 5 free petals, valvate in bud, with conspicuous hairs on the inner surface; stamens twice as many as the petals, filaments usually narrow, anthers linear to oblong, 2-theous, dehiscent longitudinally; a disk absent; ovary superior, 3- or 5-chambered throughout the height of the ovary, ovules pendulous from the central axis, with 1 integument, style narrow, stigma simple or slightly lobed. Fruit a globose to ellipsoid drupe, yellow to deep purple, often with a juicy edible pulp, seed with a small embryo at the apex of the fleshy endosperm.



A circumtropical genus of eight species of which only one is known from Central America. The presence of spines, articulate simple leaves often borne on short shoots, the free petals densely hairy within, and the ovules pendulous from a central column defining three or four separate locules help distinguish these plants. The genus is named in honor of Francisco Ximenez, who, in 1615, published an important work on the plants and animals of Mexico.

***Ximenia americana* L., Sp. Pl. 1193. 1753. Figure 3.**

Shrubs and small trees to 7 m tall, branches often with thick spines formed by modified axillary branches, leafy internodes (0) 0.5–4 cm long, 1.5–6 mm thick, with longitudinal ridges in very early stages but soon becoming terete, pale grayish and lenticellate in age, short shoots with clustered leaves often present. Leaves alternate, usually in a spiral, clearly articulate at the base, petioles 3–8 mm long, with 2 longitudinal adaxial ridges forming a narrow sulcus above that is minutely puberulent within; laminae (1.5) 3–8 (11) cm long, (1) 1.5–4 (5) cm broad, elliptic to ovate-elliptic, acute to obtuse at the apex and slightly retuse with a small mucro at the tip, acute to obtuse at the base, margins entire and decurrent on the petiole, the laminae drying stiffly chartaceous but usually very brittle and often dark in color, smooth and glabrous above and below, the 3–6 pairs of major secondary veins becoming obscure in the distal half of the lamina. Inflorescences 1 to several in the axils of leaves or fallen leaves, of 3–12 flowers in cymose, umbellate or racemose arrangements, 1–3 cm long, the flowers often in groups of 3, primary peduncles 7–15 mm long, pedicels 2–6 mm long, subtended by minute (0.5 mm) deciduous bracts; flowers ca. 5–10 mm long, glabrous on the outside, white or cream-colored but usually drying dark, calyx forming a very shallow (0.5 mm) broad (1–1.5 mm) cup with 4 (3) blunt teeth or lobes, the margin erose; petals usually 4, liguliform, 6–8 mm long, 1–1.5 mm broad, valvate in bud, and becoming reflexed, with dense tomentulous hairs 1–2 mm long on the inner surface, these white but turning reddish brown; stamens 8, equal, glabrous, filaments 3–5 mm long, anthers linear, 3–4 mm long, ca. 0.7 mm broad, ovary 3–4 mm long and 1–1.5 mm in diameter, glabrous, style 3–4 mm long, stigma simple. Fruit a yellow-orange drupe, 2–3 cm long, 1.5–2.5 cm in diameter, ellipsoid, edible but with an acid taste.

Plants of seasonally dry deciduous and semideciduous forest formations of the Pacific slope below 300 m elevation in Costa Rica; flowering material has been collected from January to April, and fruit has been collected from March to May. The species is pantropical.

*Ximenia americana* is recognized by the pale grayish branches often bearing thick spines and leaves clustered on short shoots, small leaves with a minutely mucronate tip and clearly articulate base, flowers with long hairs on the interior of the petals, and the acid-tasting fruit. The small stature, deciduous leaves, and restriction to the seasonally dry Pacific lowlands are further distinctions. The indigenous name *Tsu-kra* has been recorded from the Boruca area (*Pittier 11983*). The Central American representatives of this species have been placed in variety *americana* by DeFilipps (*Trans. Illinois State Acad. Sci. 62:350–358, 1969*).

## OPILIACEAE

Trees, shrubs, or climbers, bisexual or unisexual, generally glabrous; stipules absent. Leaves alternate in a spiral, simple and entire. Inflorescences spikes, racemes, umbels, or panicles, at first enclosed in imbricate bud scales; flowers bisexual or unisexual, radially symmetrical, small; sepals united and minutely 4- or 5-lobed or reduced to a rim and not apparent, petals (or tepals if the sepals are not apparent) 4 or 5, free and valvate in bud; stamens as many as the petals and opposite them, filaments free, anthers 2-theous, a disk of 4 or 5 lobes or separate glands present outside the stamens and alternate with them; ovary superior or united with the disk and half-inferior, 1-locular with 1 ovule pendulous from a central basal placenta or erect from the base of the locule, style short or none, stigma 1. Fruit a drupe, seed with endosperm.

A family of seven or eight genera and about 50 to 60 species, mostly of African and Asian tropics. The plants are probably all root parasites. The family is closely related to the Santalaceae and Olacaceae and has been considered a part of the Olacaceae by some workers. The Opiliaceae differ from the Olacaceae in the structure of the disk, the usual reduction of the calyx, the lack of chambers at the base of the ovary, and the lack of lignified cells in the leaves. This small family resembles Olacaceae and Celastraceae in general appearance. The leaves often turn a dull or dark yellowish green on drying.

#### AGONANDRA Miers

REFERENCES: L. O. Williams, The Agonandras of Mexico and Central America. Ciencia (Mexico) 25:227–228. 1966. P. C. Standley, The North American species of *Agonandra*. J. Wash. Acad. Sci. 10:505–508. 1920.

Small trees, shrubs, or somewhat vinelike, usually dioecious, the bark generally corky and drying pale gray, often with short shoots; stipules none. Leaves alternate and articulate at the base, petiolate, the laminae generally small and ovate to elliptic, entire. Inflorescences axillary, racemes at first subtended by decussate and caducous bracts (bud scales); flowers small and unisexual, pale yellowish to greenish in color, calyx subentire or minutely 5- or 4-lobed, petals usually 4 (5), free, valvate in bud, usually caducous in the female flowers; stamens opposite the petals, filaments slender and equal, (stamens absent in the female flower, a pistillode usually present in the male flower), disk present and annular or of separate erect glands alternating with the stamens; pistil 1, superior or with the disk adnate near the base, style absent and with a single sessile stigma. Fruit a drupe with fleshy rind and stiff endocarp.

An American genus of about 20 species ranging from Mexico to Argentina and most often found in seasonally very dry habitats. The genus is recognized by the pale grayish bark, small alternate leaves distinctly articulate at the base, and the small unisexual flowers in a racemose inflorescence at first enclosed in several series of decussately imbricate bud scales.

***Agonandra macrocarpa*** L. O. Williams, Ciencia (Mexico) 24:227. 1966. Figure 3.

Shrubs or small trees to 7 m tall (also said to be vinelike), unisexual, leafy internodes 0.1–2 cm long, 0.7–2.5 mm thick, green and strongly 2- or 3-ridged in early stages, older stems with gray bark and becoming longitudinally furrowed when dry, glabrous. Leaves alternate in a spiral, petiole 4–10 mm long, ca. 1–2 mm broad with winglike margins continuous with the margin of the lamina, slightly expanded at the articulate base; laminae 2–5.5 cm long, 1–3 cm broad, elliptic to ovate-elliptic, obtuse to bluntly acute at the apex, rounded at the tip, acute to obtuse at the base, margin entire or undulate (dry) and decurrent on the petiole, the lamina drying stiffly chartaceous or subcoriaceous, glabrous and smooth above and below, venation pinnate with 3 or 4 pairs of major secondary veins. Inflorescences originating from a bud covered with 4 distichous series of imbricate bud scales (bracts) 1–2 mm broad at the base. Male racemes less than 3 cm long, the rachis essentially glabrous, with 3 or 4 ridges and 0.3–0.5 mm thick, pedicels ca. 2 mm long, the male flowers ca. 3 mm long with reflexed tepals (the calyx obscure), glands of the disk ca. 0.5 mm long, filaments 1.5–3 mm long, anthers 0.5 mm long. Female racemes less than 1 cm long, pedicels ca. 2 mm long, tepals caducous, a yellowish annular disk ca. 1.5 mm broad conspicuous beneath the ovary, pistil ca. 1.2 mm long, ovary ca. 0.6 mm thick. Fruit globose or slightly ellipsoid, ca. 2 cm long (dry), the outer fleshy exocarp drying to form a smooth coriaceous yellowish brown surface, endocarp hard and yellowish, ca. 16 mm in diameter.

Plants of the seasonally very dry deciduous (tropical dry and tropical dry-moist zone transition) forest formations below 200 m elevation in northwestern Costa Rica; flowers have been collected in January and mature fruit in May. The species



is known only from Central Honduras and the provinces of Guanacaste and northern Puntarenas in Costa Rica.

*Agonandra macrocarpa* is recognized by the small alternate leaves articulate at the base, unusual inflorescence buds, minute unisexual flowers in small racemes, and distinctive fruit. The seasonally very dry habitat, grayish corky stems, and glabrous parts further distinguish this species, which resembles some of our species of Olacaceae. This species is apparently quite rare, with only three collections known from Costa Rica: Brenes 22481 near Los Loros (Puntarenas), and *Daubenmire* 755 and *Opler* 508, both from near Cañas. *Agonandra obtusifolia* Standley of northern Central America and Mexico has minutely puberulent stems, whereas *A. brasiliensis* Benth. & Hooker has longer finely puberulent inflorescences and smaller fruit. Our species is closely related to *A. racemosa* (DC.) Standley of Mexico and northern Central America, which has smaller fruit. The genus is poorly represented in collections, and species designations can only be regarded as first approximations.

### LORANTHACEAE sensu lato

by William Burger and Job Kuijt

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Shrubs or small trees, unisexual or bisexual, usually leafy hemiparasites with chlorophyll, erect or scandent, parasitic on the aerial stems of the host or rarely terrestrial and root parasites (as in *Gaiadendron*), usually parasitic on the stems of dicotyledonous trees and shrubs, attaching to the host by means of a haustorium (that developed from the radical of the seed), sometimes with additional haustoria on epicortical roots, stems sometimes with thickened or articulate nodes. Leaves present or reduced to small scale leaves (squamate) and apparently absent, usually opposite or subopposite, rarely whorled (some *Psittacanthus*) or rarely alternate throughout (*Antidaphne*, *Cladoclea*), simple, glabrous, often articulate at the base, laminae usually very stiff and drying brittle, with entire or undulate margins, venation pinnate to palmate. Inflorescence basically an unbranched axis with sessile or pedunculate flowers in groups of 2 (diads), 3 (triads), or solitary (monads), the flower groups borne in a spicate, racemose, or paniculate arrangement, the flowers emerging from depressions in the rachis in some genera, bud scales enclosing young inflorescences in some genera, bracts subtending the flowers or flower groups (monads, diads, triads, etc.); flowers bisexual or unisexual, radially symmetrical or nearly so, perianth present (absent only in male *Antidaphne*), floral morphology quite variable (see under segregated families below), stamens usually as many as the perianth parts and opposite them, pistil 1 and usually inferior, locule 1 or none, the ovule solitary and often not clearly differentiated, style and stigma 1. Fruit a 1-seeded berry with a layer of viscous tissue, often dispersed by birds, endosperm present in all but *Psittacanthus*, the endosperm with or without chlorophyll, cotyledons 2 or rarely as many as 12 (in species of *Psittacanthus*).

While obviously related, the plants included here represent a wide range of floral morphology and appear to include several different parallel lineages with unusual adaptation to the parasitic life-style. The reduction of the ovarian cavity and simplification of tissues of the ovule are probably associated with the evolution of a fruit that germinates on the host and develops parasitizing roots.

Recent students of these plants are agreed that they are better treated as several smaller families (see Kuijt, 1968, referred to above).

The plants included in this alliance (Loranthaceae in a wide sense) are usually easy to recognize because of their shrubby epiphyte-resembling habit and parasitic attachment to the aerial stems of the host. The very stiff, usually opposite leaves with entire or undulate margins and lack of pubescence are also characteristic. *Gaiadendron*, a root parasite often found as a terrestrial tree, superficially resembles our native species of Proteaceae, as do some of our larger species of *Psittacanthus*. *Cladocolea* and *Antidaphne* have consistently alternate leaves, whereas the apparently naked flowers of *Antidaphne* are quite unique.

The genera of the Loranthaceae in a wide sense (*sensu lato*) are here placed under the following families and in the following order: Eremolepidaceae, Loranthaceae in a narrow sense (*sensu stricto*), and Viscaceae. The following key treats all these plants. Additional keys will be found under Loranthaceae (*sensu stricto*) and Viscaceae. The figures of Eremolepidaceae and Loranthaceae (*sensu stricto*) are under the latter family, while the illustrations of Viscaceae are with the keys to that family.

#### KEY TO THE LORANTHACEAE IN A WIDE SENSE IN COSTA RICA

##### Genera and species without family designation

will be found under the Loranthaceae in a narrow sense

- 1a Leaves always alternate on all the stems, foliage leaves present.....2a
- 1b Leaves opposite, whorled, or occasionally alternate with some opposite or sub-opposite leaves present, or the leaves reduced to opposing pairs of scale leaves and foliage leaves absent.....3a
- 2a Flowers apparently bisexual with conspicuous male and female parts in the same flower (but the stamens or the pistil nonfunctional); perianth of 4 conspicuous petals, style at least 4 mm long; spikes without distal leaflike parts..... *Cladocolea*
- 2b Flowers obviously unisexual, possessing organs of only 1 sex, petals absent in the male flower and scalelike (2) in the female, style less than 1 mm long; female spikes often with small distal leaves; (Eremolepidaceae)..... *Antidaphne*
- 3a Flowers solitary in axillary positions on main stem, or borne singly on spikes and racemes, not found in diads, triads, or in longitudinal or whorled series .....4a
- 3b Flowers borne in diads or triads on spikes and racemes or in longitudinal or whorled arrangements on thick spikelike axes .....5a
- 4a Inflorescence a raceme, the individual flowers pedicellate, the pedicel supporting a bract and 2 fused bracteoles beneath the flower, foliage leaves present  
*Struthanthus panamensis*
- 4b Inflorescence of 1 to several flowers borne in the leaf axils; normal foliage leaves absent, scale leaves present. Doubtfully present in Panama and not recorded from Costa Rica ..... *Ixocactus*
- 5a Flowers obviously borne in diads (groups of 2) or triads (groups of 3) and pedunculate or sessile on relatively thin (1–3 mm) axes, the diads and triads clearly separated from each other .....6a
- 5b Flowers borne in longitudinal ranks (or occasionally in whorls or forming rounded flat groupings) on relatively thick (2–5 mm) spikelike axes, the flowers rarely in clearly isolated groups of 2 or 3, the flowers often partly sunken into the axis of the inflorescence.....10a
- 6a Flowers more than 1 cm long, perianth bright red, orange, or yellow, bisexual, the flowers occasionally smaller and subtended by leaflike bracts in *Gaiadendron*.....7a
- 6b Flowers less than 1 cm long, perianth dull yellow to dark red, bisexual or unisexual, never subtended by small leaflike bracts.....8a

- 7a Flowers golden yellow, subtended by green leafy bracts 3–20 mm long; terrestrial or growing on branches of trees. . . . . *Gaiadendron*
- 7b Flowers at least partly bright red or orange, subtended by a cupulate pedicel apex and without leaflike bracts; parasites of aerial stems. . . . *Psittacanthus*
- 8a Flowers bisexual, both the pistil and anthers functional, perianth dark red or dull yellow (in ours), inflorescences axillary and racemose or terminal and paniculate . . . . . *Phthirusa*
- 8b Flowers functionally unisexual, organs of both sexes may be present but either the stamens or the pistil not functional, the male flower buds usually thickened distally with the fertile anthers, the female flowers with tubular flower buds and the anthers absent or reduced, perianth yellowish to dull white. . . . . 9a
- 9a Filaments thin or the anthers subsessile; inflorescence always a simple racemose or spikelike axis with sessile or pedunculate diads and triads of flowers  
*Struthanthus*
- 9b Filaments thick, the upper ones with lateral depressions; inflorescence often a paniculate arrangement at the ends of twigs. . . . . *Phthirusa adunca*
- 10a Perianth parts usually 6, the flowers in 4 vertical (longitudinal) ranks on the thick inflorescence axis, with 2 minute bracteoles subtending each flower and usually found within the floral depression; spikes without distinct internodes; foliage leaves present. . . . . *Oryctanthus*
- 10b Perianth parts usually 3, the flowers variously arranged on the spike, the individual flowers not subtended by minute bracteoles; spikes with distinct internodes defined by opposite pairs of scale leaves (also called bracts); (Viscaceae). . . . . 11a
- 11a Anthers unilocular; plants with or without foliage leaves; flowers in single or multiple longitudinal ranks (series) above each scale leaf (bract). the arrangement of flowers on the internode often somewhat irregular; from 1,500–3,500 m in Costa Rica. . . . . *Dendrophthora*
- 11b Anthers bilocular; plants with foliage leaves; flowers always in multiple longitudinal ranks above each scale leaf, flowers usually in regular ranks on the internode; from sea level to 3,000 m in Costa Rica . . . . . *Phoradendron*

## EREMOLEPIDACEAE

REFERENCE: Job Kuijt, Mutual affinities of Santalalean families. *Brittonia* 20:136–147. 1968.

Shrubs, epiphyte-like hemiparasites, unisexual (or bisexual in some species of *Eremolepis*), epicortical roots produced in young stages (or possibly lacking in *Eubrachion*). Leaves alternate and simple but reduced to scalelike squamae in *Eubrachion*, petiolate, the lamina stiff with entire margin. Inflorescence spicate or racemose, at first enclosed in a conelike bud of spirally arranged imbricate and scarious bud scales, the female inflorescence often continuing with new vegetative growth distally in *Antidaphne*; flowers very small and unisexual, sessile or the male pedicellate in *Antidaphne*, with a single perianth whorl or apparently naked, the male flowers 2- to 4-parted, a perianth absent in *Antidaphne*, the stamens opposite the perianth parts in *Eremolepis* and *Eubrachion*, filaments present and free, anthers 2-thecous and dehiscent longitudinally; the female flowers 2- or 3-parted, ovary inferior (apparently half-inferior in *Antidaphne* and with 2 or 3 minute deciduous perianth parts borne halfway up the pistil), locule 1, style 1, stigma capitate. Fruit a small 1-seeded sessile berry, the endosperm with some chlorophyll in *Antidaphne*, embryo with 2 cotyledons, viscous layer of the berry formed between the vascular bundles of the perianth and the bundles of the ovary.

A small family of three genera ranging from southern Mexico and the largest Caribbean Islands through tropical South America. The Eremolepidaceae are represented in our area by a single species of *Antidaphne*. These plants are easily recognized because of their hemiparasitic habit on the aerial stems of host plants, stiff alternate leaves, inflorescences emerging from buds with imbricate and alternate bud scales, and the very small, naked or virtually naked unisexual flowers.

## ANTIDAPHNE Poeppig and Endlicher

Shrubs, hemiparasites on aerial woody branches, unisexual, stems and leaves glabrous. Leaves alternate in a spiral, simple and entire, epidermal cells sclerified except around the stomata. Inflorescences at first enclosed in overlapping small bracts (resembling the scarious bud scales of Fagaceae and other temperate plants), spicate or racemose and the female inflorescences often with smaller than normal leaves distally and the inflorescence axis sometimes continuing as a woody stem, the bracts (bud scales) deciduous and subtending 1 to several small flowers. Male flowers without a perianth, pedicellate, the stamens borne from a central disklike cushion, stamens usually 2–4, filaments slender, thecae 2 and borne on opposite sides of the connective, dehiscing laterally. Female flowers with 2 or 3 usually caducous, minute, triangular tepals halfway up the ovary, pistil with a short distinct style bearing a broad and flattened crescent-like stigma. Fruit a small 1-seeded berry; endosperm pale green.

A genus of only a few species ranging in montane forests from southern Mexico, Guatemala, and Costa Rica through northern South America to Peru, Bolivia, and Brazil.

***Antidaphne viscoidea*** Poeppig & Endlicher, Nov. Gen. & Sp. Pl. 2:70, t. 199. 1838. Figure 8.

Epiphyte-like hemiparasitic shrubs 30–120 cm in diameter, unisexual, green to olive green, leafy internodes 5–20 mm long, 1–3.5 mm thick, smooth and glabrous, becoming longitudinally striate and grayish when dry. Leaves alternate in a 2/5 spiral, often articulate at the base, petioles 1–4 mm long, broad and with lateral wings continuous with the lamina margins; laminae 1.4–8 cm long, 0.7–6 cm broad, obovate or occasionally elliptic to ovate, rounded to bluntly obtuse at the apex, gradually narrowed to the attenuate or subcuneate base, margin entire and of tissue differentiated from the leaf epidermis, the laminae drying coriaceous, smooth and glabrous, venation varying from subpalmate with dichotomizing primary veins to pinnately veined with 1–4 pairs of major secondary veins, the major veins slightly raised on both surfaces when dry, obscurely punctate. Inflorescences at first resembling small axillary shoots enclosed by several series of caducous pale brown bracts resembling scarious bud scales, the inflorescences 1 to several per node, unisexual, the female often terminating in small leaves. Male inflorescences 5–15 mm long (only rarely terminating in leaves as in *Standley* 43340 at US), racemose with 4–12 nodes, each node with usually 1 (2, 3) naked flowers; male flowers 2–3 mm long (including the short pedicels), lacking perianth, stamens 2–4 and arising from beneath the edge of a central disklike cushion, filaments ca. 1 mm long, anthers dehiscing laterally with longitudinal slits. Female inflorescences spicate, at first ca. 5–10 mm long but soon becoming woody and with small leaves distally, with ca. 10 nodes, the lower nodes with caducous bracts (bud scales) and the upper with small leaves, with 1–3 flowers per node; female flowers less than 1 mm long, sessile, lacking perianth-like whorls but with 2 or 3 deciduous scalelike perianth parts attached halfway up the ovary, style very short, stigma crestlike and flattened. Fruit a berry ca. 3 mm long, ovoid, sessile on a woody rachis 2–5 cm long and terminating with leaves 1–5 cm long, the infructescence sometimes continuing to grow beyond the distal leaves and producing new axillary shoots.

Parasites of trees in moist and wet montane evergreen forest formations between (700) 1,000 and 2,000 m elevation; probably flowering throughout the year, but collected with flower or fruit primarily from December to April. The species ranges from southern Mexico to Amazonian Brazil, Peru, and Bolivia.

*Antidaphne viscoidea* is distinguished from our other shrubby and epiphyte-like parasites by the alternate leaves with variable venation, young shoots and inflorescences enclosed by overlapping caducous bud scales giving a conelike appearance, and the flowers lacking a perianth in the male or with a very minute scalelike perianth in the female.



## LORANTHACEAE sensu stricto

Shrubs or small trees, leafy hemiparasites with chlorophyll, bisexual or the flowers functionally unisexual and the plants unisexual (dioecious), parasitic on aerial stems and resembling epiphytes or a few genera parasitic on roots and terrestrial or epiphytic and parasitizing the roots of epiphytes (as in *Gaiadendron*), attaching to the host by means of roots provided with haustoria, stems sometimes with thickened nodes, glabrous or with a scurfy epidermis. Leaves usually opposite and decussate, sometimes whorled, sub-opposite and alternate leaves occasionally present, simple, often articulate at the base, laminae usually very stiff and drying brittle, with entire or undulate margins, glabrous in ours. Inflorescences usually with an unbranched axis (in ours) with sessile or pedunculate flowers in decussate groups of 3 (triads), 2 (diads), or solitary (monads), the flowers emerging from depressions in the rachis in *Oryctanthus*; flowers bisexual or functionally unisexual (and then the plants always unisexual), the perianth generally interpreted as representing 2 whorls, the outer whorl a calyculus and the inner a well-defined whorl of petals, the calyculus with small teeth or with only a thin rim (at the distal periphery of the ovary) continuous with and of the same texture as the ovary wall, inner perianth of 6 (7) petals, valvate in bud, longer than broad, often brightly colored, stamens equal in number and opposite the petals, borne on the petals, filaments present or the anthers subsessile on the petals, dehiscent by longitudinal slits, pollen usually 3-lobed; pistil with inferior ovary, locule 1 or ovary solid, ovules replaced by a central papilla in the locule, style 1 with capitate stigma. Fruit a 1-seeded berry, endosperm compound and lacking chlorophyll, cotyledons 2 or rarely as many as 12 (in *Psittacanthus*); seed surrounded by viscid tissue in all but *Gaiadendron*.

The Loranthaceae (in a narrow sense) are a largely pantropical family of about 65 genera and 900 species. None of the New World genera occur in the Old World. The definition of genera in the family is often very unsatisfactory, especially regarding South American representatives. Many neotropical species of this family were at one time assigned to the genus *Phrygilanthus* which has been shown to be a rather heterogeneous assemblage by Barlow & Wiens (1973), who have distributed all species over several other genera. Additionally, these authors have pointed out that *Phrygilanthus* is nomenclaturally illegitimate. One of the main tasks ahead is the evaluation of the resultant genera in terms of various morphologic and other features. Another extremely difficult complex is present in *Struthanthus* and *Phthirusa*; few botanists, if any, have followed Baehni and Macbride's union of these two genera into one (*Struthanthus*), but no one has proposed a satisfactory separation. A special case is the remarkable *Phrygilanthus panamensis* Rizzini, occurring in Chiriqui Province, Panama. It was placed in *Struthanthus* by Barlow & Wiens (1973), a practice here accepted as expedient but not final (see under *Struthanthus*).

Among these parasitic plants, the genus *Oryctanthus*, while very distinctive, may be difficult to distinguish from the Viscaceae. Collections of *Oryctanthus* often resemble species of *Phoradendron* or *Dendrophthora* (Viscaceae) because of the solitary flowers emerging from the rachis and the fruiting rachis with longitudinal ranks of fruit or depressions left by the fruit. In contrast to Central American species of the last two genera, where series or groups of unisexual flowers are present above each inflorescence bract, *Oryctanthus* has a solitary flower in the axil of each bract, and all flowers are perfect and accompanied by two minute lateral bracteoles. *Oryctanthus* almost invariably has several epicortical roots at its base, organs which are unknown in any Viscaceae.

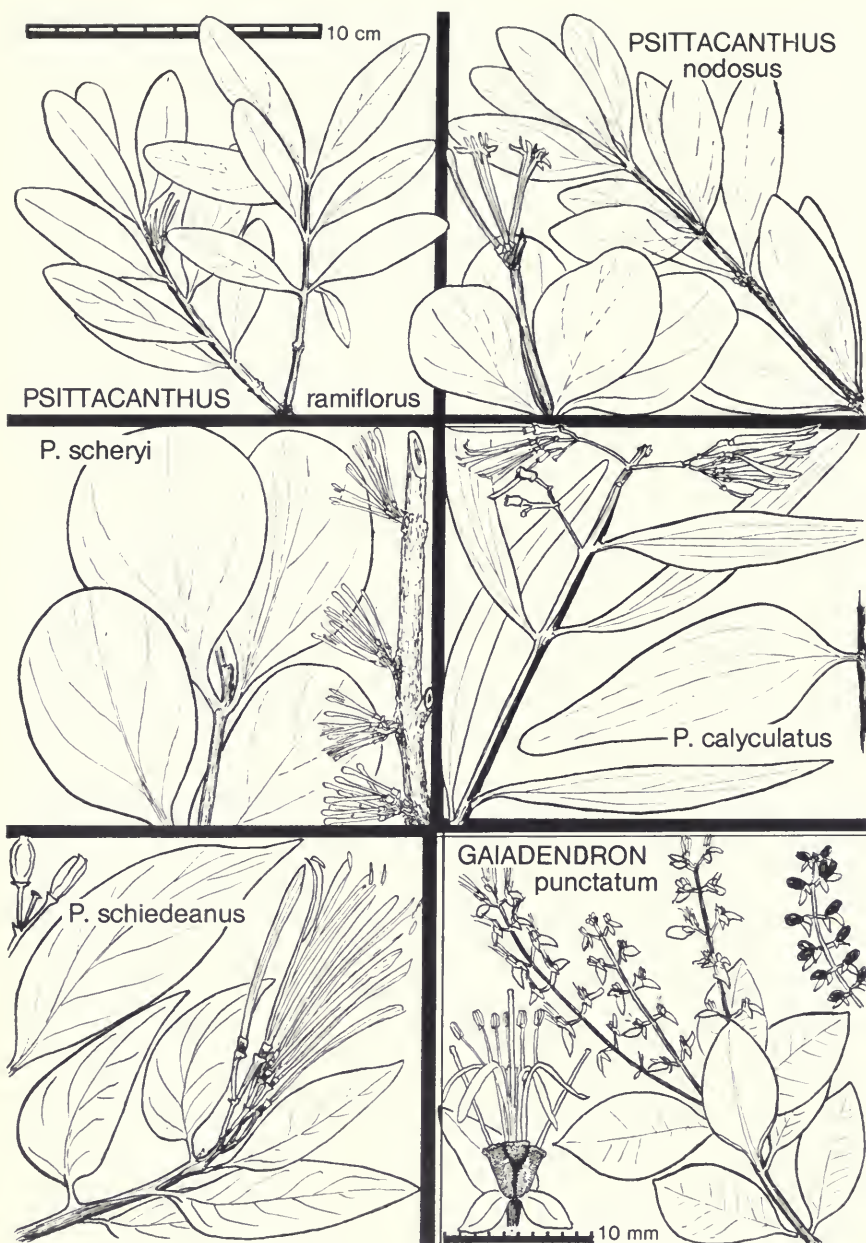


FIG. 5. Loranthaceae (s.s.): species of *Psittacanthus* and *Gaiadendron*.



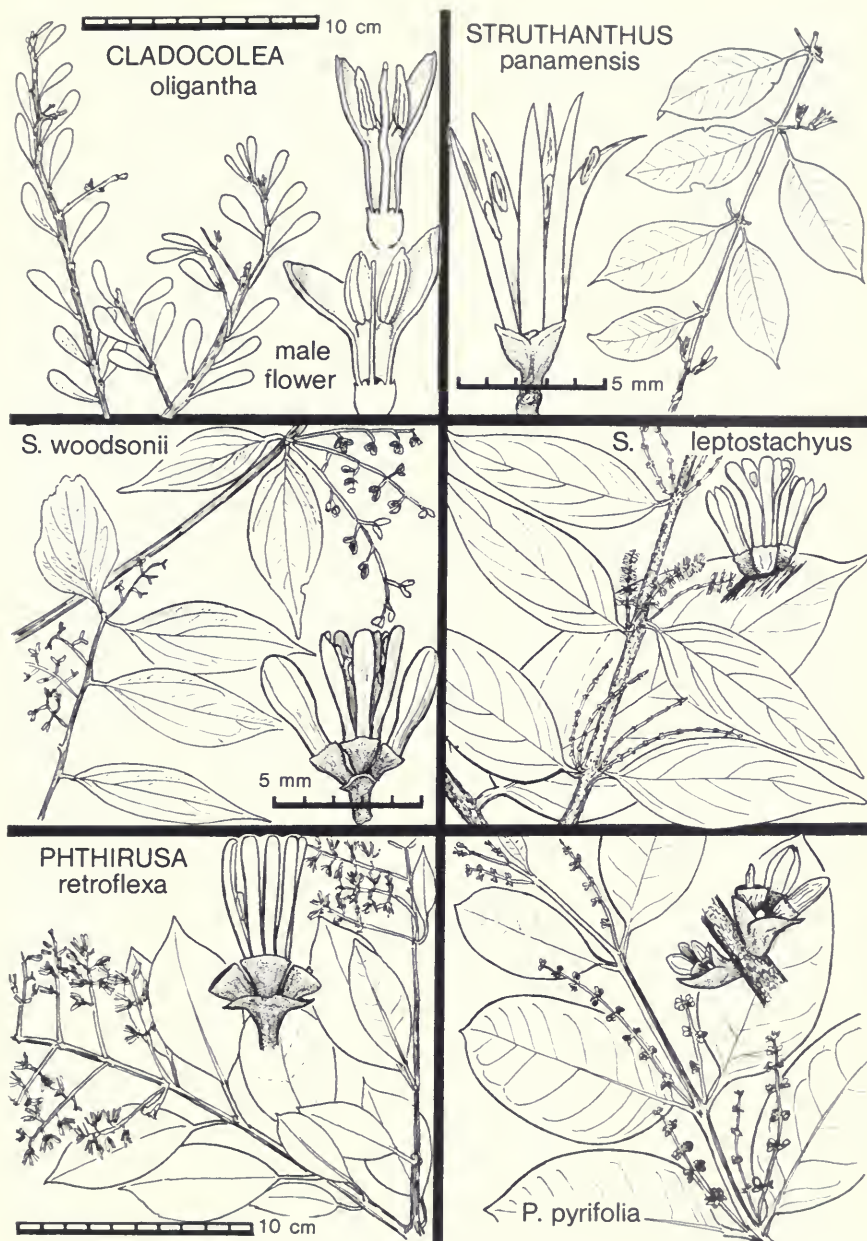


FIG. 6. Loranthaceae (s.s.): species of *Struthanthus*, *Phthirusa*, and *Cladocolea*.



FIG. 7. Loranthaceae (s.s.): additional Costa Rican species of *Struthanthus*.

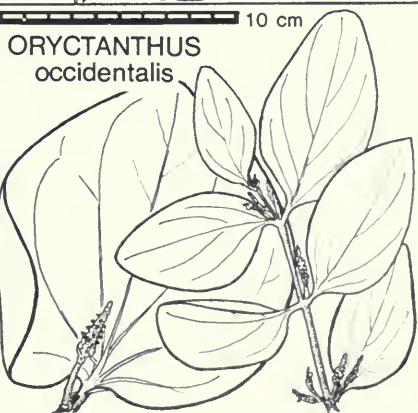
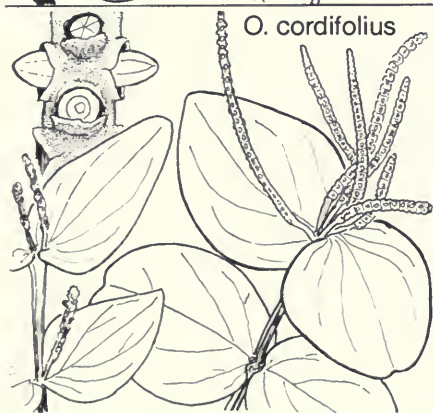
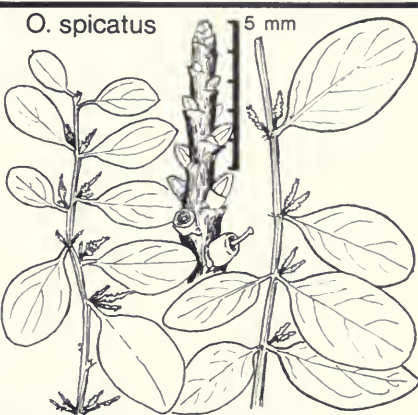
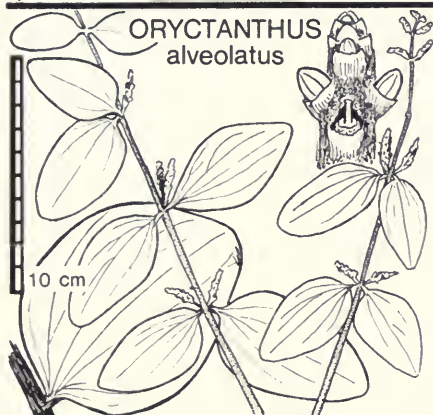
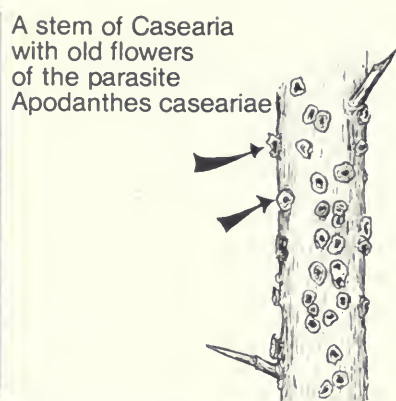
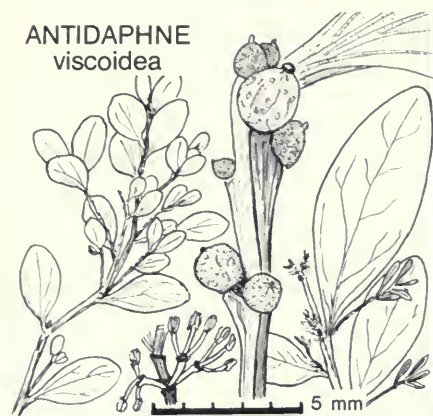


FIG. 8. Eremolepidaceae: *Antidaphne*, upper left. Rafflesiaceae: old flowers of *Apodanthes* on the stem of a *Casearia* (Flacourtiaceae), upper right. Loranthaceae (s.s.): four species of *Oryctanthus*.



## KEY TO THE COSTA RICAN GENERA OF LORANTHACEAE IN A NARROW SENSE

- 1a Flowers unisexual (aborted stamens or styles sometimes present) ..... 2a
- 1b Flowers bisexual (perfect) ..... 4a
  - 2a Phyllotaxy alternate throughout; flowers mostly single in the axis of squamate inflorescence bracts, the latter sometimes caducous ..... 3a
  - 2b Phyllotaxy decussate; flowers in paired triads ..... *Struthanthus*
    - 3a Flowers with clearly recognizable aborted organs of the opposite sex; spikes never with terminal leafy organs; petals conspicuous, always 4; style at least 4 mm long ..... *Cladocolea*
    - 3b Flowers lacking aborted organs of the opposite sex; female spikes normally with small, distal leaves which may expand into full size after flowering; petals lacking in male, less than 0.5 mm in female, 2 or 3 in number; style less than 0.5 mm long ..... *Antidaphne*
- 4a Inflorescence a spike or raceme with decussate single flowers ..... 5a
- 4b Inflorescence a spike or raceme with decussate triads or diads ..... 6a
  - 5a Flowers less than 4 mm long, sessile or even sunken in inflorescence axis, flanked by minute separate bracteoles within the rachis cavity; pollen with 3 circular depressions on each hemisphere ..... *Oryctanthus*
  - 5b Flowers more than 6 mm long, sessile in a cup made up of primary bract and 2 conspicuous bracteoles, this compound structure elevated on a 1-mm long pedicel; pollen lacking depressions ..... *Struthanthus panamensis*
- 6a Flowers less than 4 mm long; epicortical roots from base of plant ..... *Phthirusa*
- 6b Flowers longer than 4 mm; basal roots absent or resembling those of normal terrestrial plants ..... 7a
  - 7a Floral bracts green and foliose, flowers golden yellow; plants either of true epiphytic habit or terrestrial; fruit with abundant, grooved endosperm ..... *Gaiadendron*
  - 7b Floral bracts never bright green and foliose; flowers always with some red; plants parasitic on tree branches, lacking any epicortical or other roots; fruit lacking endosperm ..... *Psittacanthus*

## CLADOCOLEA Van Tieghem

REFERENCE: Job Kuijt, The genus *Cladocolea*. J. Arnold Arbor. 56:265–335. 1975.

Erect or scandent shrubs, hemiparasitic on aerial stems, bisexual or unisexual, lateral branches and inflorescences often emerging in a pseudoendogenous fashion, glabrous or puberulent in early stages; epicortical roots absent or present, on stems or at the base of the plant. Leaves opposite and decussate, alternate, or irregularly arranged, simple and entire, sometimes reduced to scales. Inflorescences usually a determinate spike, a capitulum, dichasium, or raceme, in some species the terminal flower is lost and in a few the inflorescence is reduced to a solitary flower with a pair of bracts, inflorescences usually axillary to leaves or fallen leaves; lateral flowers borne in the axils of scalelike or leaflike bracts but without bracteoles. Flowers bisexual or functionally unisexual with organs of the nonfunctional sex often well developed, mostly green to yellow in color, sessile or pedicellate, 4-, 5-, or 6-parted, stamens borne on the petals, monomorphic or dimorphic within the flower, anthers 4-thecous, pollen rounded-triangular, style straight or often geniculate or curved distally. Fruit a 1-seeded berry with endosperm, embryo dicotyledonous, elongate or globose, the haustorial disk weakly developed.

The genus *Cladocolea*, with 23 species, is centered in Mexico north of the Isthmus of Tehuantepec. A single species ranges to Panama in a (presently) disjunct distribution, and four species occur in tropical South America. The genus is distinguished from closely allied plants by the terminal floret (determinate inflorescence) and by the lack of bracts (bracteoles may be present). Most of the species of the genus have bisexual flowers, but our species has functionally unisexual flowers that may appear to be bisexual. The genus *Cladocolea* is closely related to *Struthanthus*, especially species such as *S. orbicularis* and *S. polystachyus*.

**Cladocolea oligantha** (Standl. & Steyermark.) Kuijt, J. Arnold Arbor. 56:317. 1975. *Struthanthus oliganthus* Standley & Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. 23:154–155. 1944. Figure 6.

Small shrubs, branch parasites, unisexual, few branched with relatively straight stems, terete, becoming dark brown and often with transverse lenticels; no basal or stem roots seen. Leaves alternate, gradually narrowed at the base and the petiole (not clearly differentiated) ca. 2–4 mm long and 0.5–2 mm thick; laminae 2–3.5 (4.5) cm long, 0.8–1 (1.6) cm broad, oblanceolate or occasionally lanceolate, apex acute or rounded, attenuate at the base, venation usually obscure, pinnate or subpalmate. Inflorescences of 2 kinds: (1) the primary inflorescences borne on the current year's growth are mostly solitary in the axil of a leaf with usually simple 3-flowered dichasia borne on peduncles 4–5 (10) mm long and 1 mm thick with the flowers borne in 1 plane, and (2) the secondary inflorescences (very similar to the primary but borne on the year-old growth) with 4–6 flowers borne in a congested spiral at the apex of a short peduncle and having a single terminal flower, the secondary inflorescence subtended by 1 or 2 secondary leaves that resemble primary foliage leaves but developed later. Flowers functionally unisexual, apparently bisexual but the anthers of female flowers nonfunctional and the male flowers with a prominent style but lacking a functional stigma, male and female flowers of about the same size and form, ca. 5 mm long and 2 mm thick in bud before anthesis, said to be reddish, 4-parted, anthers 1.5 mm long and subsessile halfway up the petals, 4-thecous with a projecting connective, style at least 4 mm long, stigma inconspicuous. Fruit red becoming black, ovoid, ca. 7 mm long and 5 mm in diameter, smooth, embryo nearly 4 mm long, with 2 cotyledons.

Epiphyte-like hemiparasites found between 800 and 2,000 m elevation in Guatemala and Mexico and from near sea level in Panama. The species ranges from central Mexico to central Panama, but has not been collected in El Salvador, Honduras, Nicaragua, Costa Rica, or the westernmost provinces of Panama. The species is usually found on trees of the Burseraceae, but is also recorded on Leguminosae.

*Cladocolea oligantha* is recognized by the shrubby parasitic habit (usually on trees of the Burseraceae), the small oblanceolate alternate leaves, the small inflorescences with three to six congested flowers at the apex of the peduncle, and the flowers that appear to be bisexual but are functionally unisexual.

#### GAIADENDRON G. Don

Shrubs or trees to 14 m tall, terrestrial or epiphytic, hemiparasites on the roots of shrubs or herbs. Leaves opposite or subopposite, petiolate, usually dark green, thick, minutely punctate beneath. Inflorescences raceme-like panicles with a single main axis bearing usually opposite triads of flower, the triads short-pedunculate, the flowers each subtended by a bract, larger bracts leaflike; flowers bisexual and regular, narrow and tubular before anthesis, ovary inferior with a short calyculus, the epigynous perianth parts (petals) 6 or 7, free and often recurving, bearing the adnate stamens, anthers dorsifixed and versatile, dehiscent longitudinally. Fruit a berry, subtended by the persisting bracts.

A very small genus ranging from the mountains of Nicaragua southward to Peru. These plants resemble some of our native Proteaceae as well as species of *Psittacanthus* and *Struthanthus* (q.v.).

**Gaiadendron punctatum** (R. & P.) G. Don, Gen. Syst. 3:431. 1834. *Loranthus punctatus* Ruiz & Pavon, Fl. Peruv. & Chil. 3:47, pl. 277a. 1802. *G. poasense* Donn. Sm., Bot. Gaz. 56:61. 1913. Figure 5.

Shrubs or small trees, hemiparasites, epiphytic or if terrestrial often on disturbed sites, bisexual, leafy internodes 5–40 mm long, 1.5–6 mm thick, glabrous, longitudinally ridged and grayish in age, terete. Leaves opposite or subopposite, petioles 4–10 mm long, 1–2 mm

thick, sulcate above, revolute margin of the lamina base continuous with the margins of the petiole; laminae 3–8 (10) cm long, 1.3–4 (4.7) cm broad, elliptic or somewhat obovate, usually obtuse at the apex and the tip bluntly rounded, acute to obtuse at the base, margin entire and revolute (especially near the petiole), the laminae drying subcoriaceous, smooth on both surfaces and often lustrous above, glabrous, the 6–16 pairs of major secondary veins often obscure on both surfaces or slightly impressed above, small dark punctate dots usually visible on the lower surface. Inflorescences 1–3 in the axils of leaves or several terminal (and occasionally causing a forked growth pattern), usually near the ends of twigs, 4–8 (14) cm long, raceme-like panicles with a single prime rachis and up to 16 triads often in opposite pairs, the triads on peduncles 1–3 mm long with 2 shorter (3–8 mm) bracts subtending the lateral flowers and a larger (5–20 mm) bract subtending the median flower. Flowers bisexual, perianth of 6 (7) parts, 7–12 (20) mm long, narrow and hooked apically, golden yellow to orange-yellow, recurved after anthesis, filaments borne halfway up the perianth, free portion variable in length, anthers (0.5) 0.7–1.5 (2) mm long, versatile; ovary inferior, ca. 3–4 mm long with a short (0.3 mm) flared calyculus, ca. 1 mm thick, style to 15 mm long, stigma simple. Fruit often in triads subtended by the persisting bracts and on peduncles to 10 mm long, orange berries 7–10 mm long, ellipsoid or slightly obovoid (dry), apically blunt, endosperm with as many lobes (in cross section) as the flower had perianth parts, embryo with 2 (3) cotyledons.

Plants of the evergreen montane forest formation between (800) 1,600 and 2,800 (3,000) m elevation; flowering throughout the year, but collected most often between October and April in Costa Rica. The species ranges from Nicaragua southward to Peru.

*Gaiadendron punctatum* is recognized by its narrow flower with showy orange and recurving perianth parts, flowers usually borne in threes on an unbranched raceme-like axis, conspicuous floral bracts (especially those of the central flowers), and lustrous leaves. The plants and their flowers resemble our native species of Proteaceae, some of which occur in the same habitats. Plants of this species are parasites of herbs and small trees. These plants can be both true epiphytes and true parasites by being epiphytic and parasitizing other epiphytes, but not the supporting tree (see Kuijt, On the ecology and parasitism of the Costa Rican tree mistletoe, *Gaiadendron punctatum*, Canad. J. Bot. 41:927–938, 1963).

## ORYCTANTHUS Eichler

### Nomen Conservandum Propositum

REFERENCE: J. Kuijt, Revision of the genus *Oryctanthus* (Loranthaceae). Bot. Jahrb. Syst. 95:478–534, 1976.

Small shrubs, hemiparasites of aerial stems, bisexual, young stems terete or with longitudinal ridges, often with contiguous small lenticels or with a scurfy reddish brown surface; attached to the host by a primary haustorium and a small number of epicortical roots from the base of the plant only, or rarely such roots absent. Leaves opposite or subopposite, rarely with a few alternate leaves on a stem, symmetrical, sessile or petiolate, edge of the lamina often with differentiated tissue, venation palmate to pinnate, stellate fiber bundles of lamina often visible when leaves dry. Inflorescences short to long spikes, 1 to several in the axils of leaves or on squamate (leafless) terminal shoots and forming compound inflorescences (as in some *O. alveolatus*), the flowers in 4 longitudinal (vertical) ranks and emerging from depressions within the rachis, the depressions (pits) subtended by a floral bract that is often largely united with the thickened rachis and obscure, 2 minute lateral prophylls (bracteoles) present on each side (proximal) within the floral depression; flower small, sessile, bisexual (in ours) solitary in the depressions in the rachis, calyculus subentire, perianth of 6 free parts (petals), stamens adnate to the lower half of the perianth parts, filaments very short, anthers very small and rounded but with variably prominent connective, 4- or 2-thecous, dehiscent longitudinally; both petals and stamens dimorphic; pollen globose, triangular-rounded with 3 deep circular depressions on each hemisphere,



style slender, stigma capitate. Fruit a 1-seeded berry, ovoid to cylindrical, truncate at the apex with the calyculus prominent and often with a persistent circular perianth scar.

A genus of about 10 species ranging from southern Mexico to Brazil and Bolivia. Our species are found only in evergreen or partially deciduous life zones. The emergence of solitary flowers from depressions in the inflorescence axes in early stages is an unusual feature in the Loranthaceae (s.s.), but is superficially similar to the situation in *Phoradendron* and *Dendrophthora* of the Viscaceae (q.v.). The genus also possesses anatomical peculiarities (see Kuijt, Notes on the anatomy of the genus *Oryctanthus*, *Canad. J. Bot.* 39:1809–1816, 1961).

- 1a Young stems flattened or with longitudinal ridges, at least when young ..... 2a
- 1b Young stems terete ..... 3a
- 2a Leaves petiolate, laminae generally small (1.8–7 cm) and elliptic; stems with longitudinal ridges with rough reddish brown surface; spikes to 2.5 cm long, flowers inclined forward (toward the apex of the spike); 500–1,800 m elevation  
*O. spicatus*
- 2b Leaves sessile or subsessile, laminae usually broadly ovate, 4–14 cm long; stems lacking scurfy reddish brown ridges; spikes 2–12 cm long, flowers emerging at right angles to the spike; 0–1,000 m elevation. .... *O. cordifolius*
- 3a Spikes always axillary to foliage leaves; fruits and flowers emerging at right angles to the rachis; fruit usually constricted around the center; 0–1,400 m elevation  
*O. occidentalis*
- 3b Spikes axillary to foliage leaves but also often on squamate (leafless) terminal shoots resembling panicles; fruits and flowers inclined forwardly on the rachis (toward the apex of the spike); fruit ovoid; 0–800 (1,200) m elevation. .... *O. alveolatus*

***Oryctanthus alveolatus*** (H.B.K.) Kuijt, *Bot. Jahrb. Syst.* 95:504. 1976. *Loranthus alveolatus* H.B.K., *Nov. Gen. & Sp.*, Quarto text, 3:444. 1820. *L. amplexicaulis* H.B.K., loc. cit. 445, non DC., *Prodr.* 4:305–306. 1830. *Oryctanthus botryostachys* Eichl., *Fl. Brasil.* 5, pt. 2:89–90. 1868. Figure 8.

Small shrubs, usually less than 1 m in diameter, leafy internodes (1) 2–8 cm long, 1.3–4 mm thick, bark flaking off or rough and scurfy on young stems and inflorescences, reddish brown, terete. Leaves opposite or subopposite, petioles 0–4 mm long, 1–2 mm broad, flat or slightly sulcate above, scurfy margins of the lamina continuous with the upper edges of the petiole; laminae 2–8 (10) cm long, 1.5–5 (9) cm broad, narrowly to broadly ovate or suborbicular in the larger leaves, bluntly obtuse to rounded at the apex, obtuse to rounded at the base, margin entire and occasionally undulate (dry) with a distinct edge of differentiated slightly roughened or scurfy reddish brown tissue, the laminae drying stiffly chartaceous to subcoriaceous, smooth and glabrous, venation palmate to subpalmate with 3–7 primary veins, the major veins slightly raised above and usually obscure below. Inflorescences 1 or a few in the axils of leaves or at nodes in long terminal squamate shoots that resemble a racemose panicle, spikes 1–4 (6) cm long, peduncle less than 3 mm long, rachis 1.5–3 mm thick, terete, reddish brown with rough or scurfy texture; flowers emerging from deep depressions in the rachis, inclined forwardly at an angle of ca. 45°, alternating in 4 vertical ranks, perianth 1–1.5 mm long, green on the outside and reddish within. Fruit becoming 5 mm long and 3.5 mm thick, ovate, lower half white, upper half dark green, truncated at the apex, the mature fruit usually angled forwardly as in the flowers.

Epiphyte-like hemiparasites of evergreen wet lowland forest formations usually below 1,000 m elevation; probably flowering throughout the year, but collected only between January and August. The species ranges from central Costa Rica on both the Caribbean and Pacific coastal plains to Brazil and Bolivia.

*Oryctanthus alveolatus* is recognized by the sessile to short-petiolate leaves, the scurfy reddish brown young stems that are always terete, and the relatively short spikes that are often found in opposite groups or pairs on terminal leafless stems that resemble open compound inflorescences. In Costa Rica, *O. alveolatus* seems to

fall rather clearly into two categories corresponding to what has been known as *O. amplexicaulis* and *O. botryostachys*. The former has nearly orbicular sessile leaves and a terminal compound inflorescence; the latter bears more ovate leaves with short, stout petioles, and seems to produce axillary inflorescences only. In South America, however, no such distinction can be maintained, and the present conservative arrangement is therefore considered advisable for Costa Rica.

***Oryctanthus cordifolius*** (Presl) Urban, Bot. Jahrb. Syst. 24:30. 1898. *Viscum cordifolium* Presl, Epim. Bot. 253. 1849. Figure 8.

Large shrubs, leafy internodes 3–12 cm long, 1.8–6 mm thick, with a roughened or minutely striate surface in early stages (dry), with 2 (4) longitudinal ridges and somewhat flattened but soon becoming terete. Leaves opposite, sessile or subsessile with the petiole obscured by the basal lobes; laminae 4–14 cm long, 3–12 cm broad, narrowly to broadly ovate or suborbicular, bluntly obtuse to rounded and emarginate at the apex, truncate to rounded and cordate at the base, margins entire and somewhat revolute, tissue of the edge differentiated, usually brownish and smooth, the laminae drying very stiffly chartaceous to subcoriaceous, smooth and glabrous, dark green and lustrous in life, venation palmate or subpalmate with 5 or 7 primary veins (occasionally pinnate), the major veins arcuate ascending, prominent above and somewhat obscure beneath. Inflorescences 1–3 in the axils of leaves, 2–12 cm long, peduncles 4–20 mm long, brownish and smooth; flowers sessile in depressions of the spike at right angles or slightly angled toward the apex, the 4 vertical ranks of closely spaced flowers often producing an alternating position in flowers of adjacent ranks, perianth ca. 2.5 mm long, red, ovary usually included in the depression at anthesis. Fruit becoming 5 mm long and 3 mm thick, ovoid to somewhat thickened above and obovoid, becoming dark maroon or black, smooth or occasionally muricate near the truncated apex.

Epiphyte-like hemiparasites of evergreen wet forest formations between sea level and 1,000 m elevation on both the Caribbean and Pacific sides of Costa Rica; probably flowering throughout the year, but collected only from February to April and in August and September. The species ranges from southern Mexico to Colombia.

*Oryctanthus cordifolius* is recognized by its strictly opposite sessile and subcordate leaves, young stems with longitudinal ridges, fruit becoming over 5 mm long (3 mm dry), and the spikes often becoming more than 8 cm long. This species is very similar to *O. occidentalis*, and occasionally, collections seem to be intermediate between the two. However, this may be due more to the variability within populations of *O. cordifolius* than to a close relationship.

***Oryctanthus occidentalis*** (L.) Eichler, in Martius, Fl. Brasil. 5, 2:89. 1868. *Loranthus occidentalis* L., Amoen. Acad. 5:396. 1760. Figure 8.

Small shrubs ca. 1 m long, leafy internodes (1) 2–7 (10) cm long, (0.7) 1.2–3 (5) mm thick, terete, with a scurfy reddish brown surface when young and often with many lenticels; epicortical roots slender. Leaves opposite or subopposite, petioles (0) 2–6 mm long, 1.4–4 mm broad, somewhat sulcate above with wings formed by the decurrent lamina margins; laminae 3–9 (16) cm long, 2–8 (14) cm broad, elliptic to elliptic-ovate or ovate, very broadly ovate in the unusually large leaves, bluntly obtuse to rounded at the apex, obtuse to rounded (truncate to subcordate in the very large laminae) at the base, margin entire and with differentiated rough brownish tissue along the edge, slightly revolute near the petiole, laminae drying very stiffly chartaceous to coriaceous, smooth and glabrous, the 1–3 pairs of major secondary veins arising from the lower  $\frac{1}{4}$  of the midvein, arcuate ascending, usually slightly raised above and obscure beneath. Inflorescences axillary to the current foliage, 2–6 spikes per leaf axil, 8–30 mm long and elongating in fruit to as much as 10 (15) cm, peduncles 2–15 (25) mm long, 0.8–1.6 mm thick, scurfy brown; flowers usually emerging at right angles to the rachis, closely approximate in 4 vertical ranks of circular

depressions, perianth 1–2 mm long, yellowish orange to red, anthers 4- (rarely 2-) celled. Fruit 2–3 mm long, cylindrical and abruptly truncate at the apex, ca. 1.7 mm in diameter (dry), yellowish at the base, green above but with the calycular ring sometimes becoming thickened and red (in ours), closely spaced circular depressions left by the falling fruit.

Epiphyte-like hemiparasites of evergreen moist and very wet forest formations from sea level to 1,000 (1,400) m elevation; flowering throughout the year, but collected most often in January and February and from May through August. The species ranges from Costa Rica to Colombia with a morphologically distinct population on the island of Jamaica (the type locality).

*Oryctanthus occidentalis* is recognized by its stiff strictly opposite leaves on terete stems, small bisexual flowers emerging in perpendicular fashion from deep depressions in the axis of the spike, and fruit somewhat constricted around the middle. The leaves vary greatly in different plants and occasionally on the same plant. The larger leaves (over 8 cm long and 6 cm broad) are not found associated with the smaller (5- by 2-cm) elliptic leaves, but many collections contain intermediate sizes.

Within Costa Rica, considerable differences seem to exist between individuals from the Atlantic and Pacific slopes. Collections from the General Valley-Golfo Dulce area have longer petioles and peduncles, larger leaves, a much more prolific production of spikes, and a fruit which lacks the tubercular distal surface (Kuijt, 1964). Some plants from this region are capable of originating as many as four or five shoots from a single root (as in *Kuijt* 2440).

*Oryctanthus spicatus* (Jacq.) Eichler, in Martius, Fl. Brasil. 5, pt. 2:89. 1868. *Loranthus spicatus* Jacq., Enum. Pl. Carib. 18. 1760. *Struthanthus guatemalensis* Standl., Field Mus. Nat. Hist., Bot. Ser. 17:237. 1937. *Oryctanthus guatemalensis* (Standl.) Standl. & Steyererm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23:40. 1944. Figure 8.

Small shrubs, ca. 50 cm in diameter but occasionally with stems 1 m long, leafy internodes 1–4 (6) cm long, 1.5–4 mm thick, with 2 or 4 longitudinal scurfy reddish brown ridges, often smooth between the ridges or entirely scurfy on the very young stems, often somewhat flattened but becoming terete in age; epicortical roots usually 3. Leaves opposite or subopposite (occasionally alternate), petioles (2) 4–8 mm long, 0.7–1.8 mm thick, slightly sulcate above with ridges continuous with the lamina margins, the lower side with a longitudinal scurfy ridge continuous with the midvein; laminae 1.8–6 (8) cm long, 0.8–2.5 (3.5) cm broad, elliptic to oblong or slightly obovate, bluntly obtuse to rounded and emarginate at the apex, acute to subtruncate at the base, margin entire and becoming somewhat revolute, edge with differentiated brown and slightly roughened tissue, the laminae drying stiffly chartaceous to subcoriaceous, smooth and glabrous but the midvein often raised and with scurfy tissue beneath (abaxially), venation pinnate with 2–4 pairs of major secondary veins arising from the lower half of the midvein and arcuate ascending, raised or obscure on either surface. Inflorescences 1 or 3 in the axils of current foliage, 0.4–2.5 cm long, peduncles 2–7 mm long, rachis ca. 1.4 mm thick (dry) with up to 24 flowers; the flowers emerging from shallow depressions in the rachis at an acute angle to the apex, perianth ca. 1.5 mm long, dark wine red. Fruit to 5 mm long and 3.5 mm thick (dry), ovoid to somewhat cylindrical, truncated at the apex, smooth.

Epiphyte-like hemiparasites of evergreen or partly deciduous forest formations between 500 and 1,800 m elevation; apparently flowering throughout the year. The species ranges from Guatemala to Peru and Venezuela, where it intergrades with the South American *O. florulentus* (Rich.) Urban. It is remarkable that the species has not yet been collected from either Nicaragua or Panama.

*Oryctanthus spicatus* is recognized by the generally smaller leaves on young stems with longitudinal scurfy ridges, the small spikes with relatively few flowers,

and the restriction to middle elevation habitats. The few flowers obscure the four-ranked nature of the flowers on the spike, leaving the old spike terete rather than four-angled as in fully mature fruiting spikes in some of the other species.

## PHTHIRUSA Eichler

### Nomen Conservandum Propositum

Erect or scandent shrubs, usually bisexual, hemiparasitic on aerial stems; rooting only from the base of the plant (in our species) or also from the stems. Leaves opposite and becoming articulate at the base (in ours), subopposite or rarely alternate. Inflorescences usually solitary in the leaf axils, on leafless terminal or lateral shoots in a few species (South America), imbricate bud scales lacking in early stages, racemose or spicate to paniculate in superficial appearance, an indeterminate thyrs of decussate dichasia (triads) in ours, the flowers borne in triads (dichasia) or rarely in monads, each triad subtended by 1 primary and 2 secondary bracts, the lateral flowers associated with 3rd- and 4th-order bractlets, bracts and bractlets often connate to form a cup at the base of the flowers, triads sessile or very short pedunculate; flowers usually bisexual, calyculus thin and entire, petals usually 6 (4), stamens of 2 lengths, usually borne on the base of the perianth parts, filaments of 2 lengths, the longer often scalloped by the pressure of adjacent anthers on the shorter filaments, anthers dehiscing longitudinally, said to produce pollen grains of a single type: triangular in shape with finely granulose exine and 3 pores, ovary with or without a locule, with only 1 functional megaspore (in ours). Fruit a 1-seeded berry, endosperm without chlorophyll.

A genus of about 30 species ranging from southern Mexico and the West Indies southward to Brazil. The genus is poorly defined and may not be distinct from *Struthanthus*. One of our species seems to be self-pollinating (see Kuijt & Weberling, The flowers of *Phthirusa pyrifolia*, Ber. Deutsch. Bot. Ges. 85:467-480, 1972).

In 1830 Martius erected the genus *Phthirusa* on the basis of a single species now placed in *Cladocolea* (Kuijt, 1975). In order to reduce nomenclatural confusion, it has been proposed that *Phthirusa* in the sense of Eichler (1868) be conserved over the original sense of Martius (see Taxon 24:389, 1975). *Phthirusa pittieri* Krause, based on a type from Colon, Panama, has proven to be *Struthanthus leptostachyus*.

### KEY TO THE SPECIES OF PHTHIRUSA IN COSTA RICA AND PANAMA

- 1a Inflorescence always simple and usually axillary (a racemose unbranched axis with pedunculate triads); flowers bisexual and less than 4 mm long; wine red to dark red or maroon; 0-1,200 m elevation and widespread ..... *P. pyrifolia*
- 1b Inflorescence often terminal and panicle-like, simple racemose inflorescences may also be present; plants and flowers said to be unisexual, flowers 4-5 mm long and yellowish; 0-1,800 m in Panama ..... *P. retroflexa*

***Phthirusa pyrifolia* (H.B.K.) Eichler, Fl. Brasil. 5(2):36. 1868. *Loranthus pyrifolius* H.B.K., Nov. Gen. & Sp. 3:441. 1820. Figure 6.**

Shrubs or vinelike, to 1 m long, often pendant, hemiparasitic epiphytes, bisexual, leafy internodes 1-7 cm long, 1.6-5 mm thick, thicker below the nodes, glabrous but often forming brownish flakes on drying, usually with 2 longitudinal ridges continuous with the petioles of the next distal node; epicortical roots arising only from the base of the plant. Leaves opposite, subopposite, or occasionally alternate, dark green and lustrous, petioles 4-20 mm long, 0.8-3 mm thick, distinct, sulcate above with adaxial ridges continuous with the lamina margins; laminae 4-14 cm long, 2-8 cm broad, elliptic to oblong, ovate or lanceolate, rounded to obtuse or less often acute at the apex, often mucronate with a small (1-2 mm) narrow tip but this readily breaking off when dry, subtruncate to obtuse at the base, margin entire and the edge drying roughened brownish, differentiated from the



epidermis, the laminae drying subcoriaceous, glabrous and smooth, venation pinnate with the 4–6 pairs of major secondary veins arising throughout the length of the midvein, the secondaries often abruptly arcuate ascending about halfway between the midvein and margin in larger leaves. Inflorescences solitary or paired in the leaf axils or from leafless terminal shoots and paniculate, usually spicate and 4–12 cm long, the triads of flowers subsessile or on very short (1–2 mm) peduncles, bracteate apically beneath the flowers, triads usually in opposite pairs 3–12 mm distant on the rachis, rachis ca. 0.8 mm thick and with minute scaly surface when dry; flowers sessile, bisexual, perianth parts ca. 1.5 mm long, wine red or maroon, ovary 1–1.5 mm long and ca. 1 mm thick, without a locule, calyculus small (0.3 mm) and slightly flaring, style simple. Fruit a blunt ellipsoidal berry, bright orange-red with yellowish apex and dark purple base, ca. 8 mm long and 5 mm thick but 3–5 mm long and 1.5–3 mm thick when dry, smooth and with a minutely (0.05 mm) reticulate surface, the triads often projecting obliquely downward (toward the base of the spike).

A common and widespread hemiparasite on tree branches in evergreen and partly deciduous forest formations between sea level and about 1,200 m elevation; apparently absent from the deciduous (tropical dry) forests of lowland Guanacaste. Flowering throughout the year in Costa Rica, but collected most often between January and August. The species ranges from southern Mexico to the West Indies and northern South America.

*Phthirusa pyrifolia* is recognized by its ridged stems, opposite and subopposite (alternate) leaves often on the same stem, pinnate venation, subsessile triads of very small flowers well spaced along the slender spikelike inflorescence, and fruit with unusual minutely reticulate surface. These plants resemble species of *Struthanthus*, but differ in having very small apparently bisexual dark red flowers and in the fact that epicortical roots are not produced from the stem, but only from the cotyledonary zone.

***Phthirusa retroflexa* (R. & P.) Kuijt**, Brittonia 32:521. 1980. *Loranthus retroflexus* Ruiz & Pavon, Fl. Peruv. 3:49–50, t. 279b. 1802. *L. aduncus* Meyer, Prim. Fl. Esseq. 149. 1818. *L. paniculatus* H.B.K., Nov. Gen. & Sp. 3:422. 1820. *L. theobromae* Willd. ex R. & S., Syst. Veg. 7:132. 1829. *Struthanthus retroflexus* (R. & P.) Blume, in Schult., Syst. Veg. 7:1731. 1830. *Phthirusa paniculata* (H.B.K.) Macbr., Field Mus. Nat. Hist., Bot. Ser. 11:17. 1931. *P. adunca* (Meyer) Maguire, Bull. Torrey Bot. Club 75:301. 1948. Figure 6.

Shrubs, the stems often scandent, unisexual, leafy internodes 0.5–4.5 (8) cm long, 1.1–4 (5.5) mm thick, terete and smooth, drying pale brown or grayish; roots borne on the stems. Leaves opposite, subopposite, or alternate, clearly articulate at the base, petioles well defined, 8–23 mm long, 1–2 mm broad, adaxial groove formed by ridges continuous with the lamina margins; laminae 3.8–8 cm long, 2.5–5 cm broad, ovate to broadly elliptic or broadly oblong, acute to short-acuminate at the apex (emarginate only where damaged during development?), obtuse to rounded at the base, margin entire, stiffly chartaceous and drying dark and brittle, glabrous, venation pinnate with 4–7 pairs of major secondary veins arising throughout the length of the midvein, often irregular in arrangement and sometimes obscure on both surfaces. Inflorescences an unbranched solitary raceme of triads in the axils of leaves or more often a compound panicle at the ends of stems (formed by the failure of distal leaves to develop), triads (occasionally diads and monads) borne on peduncles 1–3 mm long, small triangular bracts ca. 1–2 mm long borne at the apex of the peduncle beneath each flower and often deciduous; flowers unisexual(?), rather similar in size and form, perianth ca. 4–5 mm long, pale yellow, anthers ca. 1.5 mm long; ovary ca. 1.5 mm long and 1.5 mm broad at the apex, narrowed at the base. Fruit to 1 cm long, oblong and pedicellate, orange.

Hemiparasites of both evergreen and deciduous forest formations from sea level to 1,800 m elevation. Probably flowering throughout the year, but collected most



often between April and July. The species ranges from westernmost Panama to Peru and Paraguay (fide Rizzini).

*Phthirusa retroflexa* is recognized by its epiphyte-like parasitic habit, small leaves narrowed at the apex (and quite variable as regards arrangement on the stem), triads of yellow flowers, and the very unusual terminal panicle-like inflorescences in addition to simpler axillary inflorescences. Although not yet recorded from Costa Rica, this species is likely to occur near the border with Panama.

### PSITTACANTHUS Martius

Hemiparasitic shrubs, parasitizing the aerial parts of trees and shrubs, often large, bisexual, leafy stems strongly ridged to terete; epicortical roots absent, the haustorium often becoming large. Leaves opposite, whorled, or very variable in some species and ranging from alternate to whorled (often on the same stem), symmetrical to asymmetric, articulate at the base, simple and entire, glabrous. Inflorescences axillary or terminal, 1 to several per leaf axil, fasciculate at older leafless nodes in some species, primary peduncles bearing 1–3 secondary peduncles subtending the triads or diads of flowers, floral pedicels expanded at the apex to form a deep or shallow cup, the cup usually becoming asymmetrically expanded on 1 side, entire; flowers 2–10 cm long, bisexual, brightly colored and usually reddish or orange near the base grading into a yellowish apex, the calyculus little differentiated from the ovary, thin, entire or minutely denticulate, perianth forming a slender tube before anthesis, thickened distally around the anthers and in some species expanded just above the base, the 6 perianth parts separating at anthesis, filaments mostly free, of 2 lengths with the anthers superposed at 2 levels of 3 just beneath the apex of the perianth, anthers dorsifixed and versatile, slender, style long and slender with a simple slightly thickened stigma. Fruit a smooth bluish black berry.

An American genus of uncertain size that has not been revised since Eichler's work in the Flora Brasiliensis more than 100 years ago. The species are largely continental and range from Southern Mexico to Argentina. The very colorful perianth and the numerous inflorescences of some species often make the plants very conspicuous. The pedicels are expanded to form a dishlike base beneath the flowers, probably representing a fusion of bracts and bracteoles. The plants may be confused with our species of *Gaiadendron*, but other members of the Loranthaceae in a wide sense are quite different in having much smaller flowers.

- 1a Larger leaves asymmetric and with the midvein curved to 1 side; leafy stems strongly 4-angled with 4 longitudinal ribs or wings; inflorescences terminal, flowers usually in triads ..... 2a
- 1b Leaves symmetrical with the midvein usually straight; stems rarely 3- or 4-angled, soon becoming terete; inflorescences axillary or borne on older wood, flowers usually in diads ..... 3a
  - 2a Larger laminae asymmetrically ovate; flowers to 9 cm long; evergreen montane forests, 1,700–3,300 m elevation ..... *P. schiedeanus*
  - 2b Larger laminae asymmetrically lanceolate or falcate; flowers to 5 cm long; deciduous lowlands ..... *P. calyculatus*
- 3a Leaves usually in whorls of 4 and separated by long (3–12 cm) internodes; flowers 4–6 cm long on small axillary inflorescences, anthers subsessile with slender hairs from the base; evergreen forests, 500–1,000 m elevation ..... *P. nodosus*
- 3b Leaves alternate, opposite or in whorls of 3 (very rarely 4), leafy internodes 1–8 cm long; flowers 3–4 cm long; anthers on long filaments, without hairs ..... 4a
- 4a Laminae ovate to suborbicular or elliptic, to 14 cm long and 10 cm broad; inflorescences often on older stems more than 1 cm thick, primary peduncles less than 5 mm long; (1,000) 1,500–2,500 m elevation ..... *P. scheryi*
- 4b Laminae usually elliptic-oblong, to 8 cm long and 4 cm broad; inflorescences from leaf axils or on older stems not usually more than 1 cm thick, primary peduncles 4–14 mm long; 500–1,800 (2,200) m elevation ..... *P. ramiflorus*

***Psittacanthus calyculatus* (DC.) G. Don, Gen. Syst. 3:415. 1834. *Loranthus calyculatus* DC., Coll. Mem. pl. 10. 1830. *P. chrismarii* Urban, Bot. Jahrb. Syst. 24:331. 1897. Figure 5.**

Shrubs, branch parasites with the branches often long and trailing, leafy internodes 1–6 cm long, 1.7–7 mm thick, 4-angled in cross section with 4 longitudinal ribs, green but becoming gray. Leaves opposite or subopposite (occasionally alternate), decussate, dark green, asymmetric and usually somewhat curved, petioles 0–8 mm long, gradually merging with the lamina, 1–2.5 mm broad with wings continuous with lamina margins; laminae 4–15 (20) cm long, (1) 1.4–3.5 (5) cm broad, lanceolate to falcate or narrowly ovate, usually with the midvein curved to 1 side, tapering gradually to the acute or blunt apex, acute to cuneate or attenuate at the base, margin entire or undulate and decurrent on the petiole, the edge slightly differentiated, the laminae drying coriaceous, smooth and glabrous, venation subpalmate or pinnate with 2–4 pairs of major secondary veins arising from near the base of the lamina, strongly ascending, usually obscure. Inflorescences terminal with the lowest units axillary to a pair of foliage leaves, or less often axillary, paniculate, 5–12 cm long, usually with a basal peduncle 1–2 cm long and 1 or 2 secondary peduncles, peduncles of the triads (diads) 4–16 mm long, pedicels of the flowers 6–20 mm long, 0.6–1.2 mm thick, flared near the apex to form a somewhat asymmetric cup 3 mm broad enclosing the base of the ovary; flowers ca. 4 cm long before anthesis, slender but dilated at base and apex, incurved, ovary ca. 3–4 mm long including calyculus and 2.5–3 mm thick, the calyculus very slightly flared, 3–4.5 mm broad, subentire with several small notches and differentiated margin, perianth parts 3–4 cm long, ca. 1–2 mm broad, orange to red, filaments subequal, differing by ca. 4 mm in length, anthers 3 mm long, dorsifixed and versatile, stigma ca. 3.5 cm long, very slender, stigma slightly thickened. Fruit black and ellipsoid, becoming 9 mm long and 5 mm in diameter.

Colorfully flowered hemiparasites of the seasonally very dry deciduous forest formations of Guanacaste and the Nicoya peninsula; probably flowering throughout the year, but only collected from September to March in Costa Rica. The species ranges from southern Mexico to northern South America.

*Psittacanthus calyculatus* is recognized by the medium-sized bright orange-red flowers, curved narrow leaves that are opposite to almost alternate on the strongly angled gray stems, and the seasonally very dry lowland habitat. *Psittacanthus mayanus* Standl. & Steyerl. of northern Central America with smaller symmetrical leaves may prove to be no more than an unusual form of this species.

***Psittacanthus nodosus* (Desr.) G. Don, Gen. Syst. 3:417. 1834. *Loranthus nodosus* Desr., in Lamarck, Encycl. 3:601. 1809. *Aethanthus nodosus* (Desr.) Engler, in Engler & Prantl, Nat. Pflanzenfam., Nachtr. 1:136. 1897. Figure 5.**

Shrubs to ca. 1 m tall, leafy internodes (1) 3–12 cm long, 2.3–7 mm thick, terete, pale grayish with narrow longitudinal lenticels, the nodes conspicuously thickened. Leaves almost always in whorls of 4 and producing a striking verticillate appearance, symmetrical, articulate at the base, petioles 0–10 mm long, the adaxial ridges continuous with the lamina margins, ca. 2 mm broad; laminae 5–10 (12) cm long, 2–4.5 (7) cm broad, elliptic to obovate, ovate, or ovate-elliptic, bluntly acute to rounded at the apex, gradually tapering to the acute, obtuse, or cuneate base, margin entire and becoming recurved, decurrent on the petiole, the laminae drying stiffly coriaceous, glabrous and smooth but with a rough appearance, venation pinnate with 2 or 3 pairs of major secondary veins arising from the lower half of the midvein, secondary veins strongly ascending and usually obscure beneath. Inflorescences axillary, 1–6 (rarely more) per node, ca. 6–10 cm long including the flowers, peduncles and pedicels together usually less than 2 cm long, primary peduncle 2–5 mm long, 1 mm thick (dry), peduncles of the diads about the same length, pedicels ca. 5 mm long and flared at the apex to form a shallow asymmetric cup 3 mm broad; flowers 4–6 cm long, slender and straight before anthesis, ovary and calyculus ca. 4 mm long and 2 mm thick, perianth ca. 4.5 cm long, the tube 2–4 mm thick before anthesis, yellow

apically and brilliant red toward the base, filaments apparently equal, anthers ca. 3 mm long, stigma slightly thickened. Fruit to ca. 12 mm long and 8 mm in diameter, green becoming black (dry), epidermal cells apparent (0.1 mm) on the lustrous surface.

Unusual branch parasites of premontane wet forest formations between about 500 and 1,000 m elevation; probably flowering throughout the year. The species ranges from northern Costa Rica to Ecuador.

*Psittacanthus nodosus* is recognized by its large colorful flowers, round stems with distant nodes of four whorled leaves, and relatively small inflorescences. Material of this species has been mixed with *Struthanthus costaricensis* under the numbers 11458 and 11611 (Tonduz and Herb. Inst. physico-geogr. nat. costar.). Thus, we believe, the locality of Santa Maria at 1,450 m elevation may be in error and have listed the altitudinal range as lower. This species is known only from the following collections: *Lent* 2563 Rio Naranjo west of Volcan Tenorio, *Poveda* 965 Pavones de Turrialba, *Standley & Valerio* 46816 near Pejivalle, Cartago, *Tonduz* 11458 near Tuis, Cartago.

***Psittacanthus ramiflorus*** (DC.) G. Don, Gen. Syst. 3:415. 1834. *Loranthus ramiflorus* DC., Prodr. 4:308. 1830. *P. allenii* Woodson & Schery, Ann. Missouri Bot. Gard. 27:309. 1940. *P. lateriflorus* Woodson & Schery, loc. cit. Figure 5.

Shrubs, branch parasites, leafy internodes 0.1–3 (5) cm long, 2–6 mm thick, terete or angled and with longitudinal ridges in early stages but becoming terete in age, smooth and gray green but becoming rough and dark gray in age. Leaves opposite, subopposite, in whorls of 3, or alternate (often on the same stem), symmetrical, articulate at the base, petioles 2–12 mm long, 1–2 mm broad, the lateral wings continuous with the lamina margins; laminae 3–8 cm long, 1.3–4 cm broad, elliptic-oblong to narrowly elliptic, ovate-elliptic, ovate, elliptic, or obovate-elliptic, bluntly obtuse to rounded at the apex, tapering gradually or abruptly at the acute to obtuse or cuneate base, margin entire and decurrent on the petiole, becoming revolute, the laminae drying subcoriaceous, smooth and glabrous, venation pinnate, the 3 or 4 pairs of major secondary veins arising from throughout the length of the midvein. Inflorescences in leaf axils or at leafless nodes on stems usually less than 1 cm thick, 5–8 cm long, primary peduncle 4–14 mm long, peduncles of the diads 3–6 mm long, pedicels ca. 5 mm long, 0.5–0.8 mm thick and expanded at the apex to form a flattened shallow cup 2–3 mm broad; flowers 3–4 cm long, ovary ca. 3 mm long and 2 mm in diameter, calyculus thin and entire (subentire), perianth parts ca. 3–3.5 cm long at anthesis, forming a slender tube before anthesis, thickened at the apex and at the base, small projections ("ligule") at the apex of the basally expanded portion of the perianth parts on the inner surface, filaments of 2 lengths, anthers 2–3 mm long, stigma simple and very slightly thickened. Fruit not seen.

Epiphyte-like hemiparasites of trees and shrubs in premontane and lower montane wet forest formations between 600 and 1,800 (2,200) m elevation on the Pacific watershed; collected with flowers from April to December. The species, in our area, ranges from the Sierra de Tilaran in Costa Rica to Central Panama.

*Psittacanthus ramiflorus* is recognized by the usually small symmetrical leaves alternate to whorled on rounded stems and the 3–4 cm long flowers on short inflorescences that occur in leaf axils or on slender leafless stems. This species is very closely related to *P. scheryi* (q.v.), and that species may be no more than a large-leaved form of *P. ramiflorus*. *Psittacanthus dilatatus* A. C. Smith of Colombia appears to be closely related to *P. ramiflorus*.

***Psittacanthus scheryi*** Woodson, Ann. Missouri Bot. Gard. 28:426. 1941. Figure 5.

Shrubs 1–2.5 m tall, leafy internodes 1–8 cm long, 3–11 mm thick, terete and relatively

smooth, becoming rough and longitudinally striate with narrow lenticels in age. Leaves variable in position, alternate to subopposite, opposite, or in whorls of 3 (4), symmetrical, articulate at the base, petioles 4–14 mm long, 1.3–4 mm broad with ridges continuous with the lamina margins; laminae 4.5–15 (18) cm long, (2) 3–10 (12) cm broad, ovate to elliptic-ovate or occasionally narrowly elliptic or suborbicular, obtuse and blunt or rounded at the apex, abruptly or gradually narrowed at the base, margin entire, often becoming revolute and undulate, the laminae drying very stiffly coriaceous and often pale in color, smooth and glabrous, venation pinnate with the 3–6 pairs of major secondary veins arising from throughout the length of the midvein, usually obscure beneath. Inflorescences fasciculate in the axils of leaves or fallen leaves, often on older stems over 1 cm thick, to 5 cm long including flowers, primary peduncles usually less than 5 mm long, peduncles of the diads (very rarely triads) 3–6 mm long, pedicels 3–7 mm long, ca. 1 mm thick (dry), flared at the apex and forming an asymmetric cup 3–4 mm wide at its broadest; flowers ca. 3–4 cm long, ovary ca. 3 mm long and 2 mm in diameter, flared slightly at the short (0.7 mm) thin entire calyculus, perianth parts ca. 3 cm long, slender and thickened near the apex, abruptly expanded for ca. 3 mm above the base, a slight projection ("ligule") at the apex of the basally expanded portion of the perianth parts on the inner surface, orange or reddish near the base and yellow-orange apically, filaments of 2 lengths and differing by ca. 4 mm, anthers 2–3 mm long, stigma simple, very slightly thickened. Fruit ca. 12 mm long and 8 mm in diameter, ellipsoid, black and borne on red pedicels, calyculus very short on the truncate apex.

Epiphyte-like hemiparasites of wet evergreen montane (premontane wet to montane rain) forest formations between (1,000) 1,500 and 2,500 m elevation in Costa Rica; flowering throughout the year. The species, as presently understood, ranges from the Cordillera Central de Costa Rica to western Panama.

*Psittacanthus scheryi* is recognized by its fasciculate inflorescences often on older stems, slender medium-sized flowers apically yellowish, and often large thick leaves that vary from alternate to opposite or whorls of three. This species is related to *P. dilatatus* of Colombia with narrower obovate leaves, and it may be no more than a large-leaved form of *P. ramiflorus* in a wider sense. The specimens that have been placed here are being kept separate from *P. ramiflorus* because their overall appearance is quite different, and the distinctions given in the key seem to be working well with newly collected specimens.

***Psittacanthus schiedeanus*** (Schlecht. & Cham.) Blume, in Schult., Syst. Veg. 7:1730. 1830. *Loranthus schiedeanus* Schlecht. & Cham., Linnaea 5:172. 1830. Fig. ure 5.

Shrubs, to 3 m long, often high up in tall trees and conspicuous because of the bright red-orange inflorescences, leafy internodes 0.5–10 cm long, 2–9 mm thick, glabrous, 4-angled with 4 prominent longitudinal wings, nodes somewhat flattened; haustorial connections becoming 35 cm in diameter. Leaves opposite or subopposite, usually bluish green, petioles 3–20 mm long, distinct, 1–2.5 mm thick, inconspicuously winged; laminae 4–26 cm long, 2–10 cm broad, narrowly ovate (rarely lanceolate) to broadly and inequilaterally ovate, the larger laminae often very asymmetric in the lower half with the midvein curved, gradually narrowed to an acute or acuminate apex, narrowed to abruptly rounded at the often unequal base, margin entire and decurrent on the petiole, edge differentiated from the epidermal tissue, the laminae drying subcoriaceous to coriaceous, smooth and glabrous, venation pinnate with the 3–5 pairs of major secondary veins usually obscure. Inflorescence axillary or terminal at the ends of twigs (and resulting in forked growth), leafless, 10–20 cm long including the flowers, of a condensed axis 1–3 cm long bearing 8–14 triads in opposite or subopposite pairs, paniculate in general form, peduncles of the triads 12–35 mm long, bracteate at the apex by adnation, bracts broad based and ca. 2 mm long, pedicels of the flowers 10–20 (30) mm long, flaring into a cupulate apex enclosing the flower base, peduncles, pedicels, and exposed areas of buds becoming bright red or orange; flowers 8–9 cm long before anthesis, ovary ca. 4 mm long and 5 mm thick, crowned by a short (3 mm) tubular calyculus continuous with the ovary, subentire and minutely



3-toothed, perianth becoming 9 cm long and only 2–4 mm broad, linear, slightly thickened below the apex and with an acuminate tip, brilliant orange, becoming recurved, deciduous, filaments 4–6 cm long, dimorphic and differing by ca. 5 mm in length, anthers dorsifixed and versatile, ca. 6 mm long, style ca. 7.5 cm long, stigma slightly thickened. Fruit a blackish berry 1.5–2 cm long, ca. 1 cm thick, ellipsoid, on pedicels to 3 cm long; embryo with 6–12 awl-shaped cotyledons triangular in cross section.

Large epiphyte-like parasites, conspicuous when in flower in evergreen montane forests between about 1,700 and 3,300 m elevation; flowering from December to August. This species is especially common on the central Volcanos; it ranges from central Mexico to western Panama.

*Psittacanthus schiedeana* is recognized by its large and colorful slender flowers, the ridged stems, asymmetric larger leaves, and montane habitat. The number of cotyledons is unusual. The cotyledons persist for some time, becoming raised and separated from each other by the rapid expansion of the haustorial body. It is probably this species that is responsible for the majority of "rosas de palo" or "flores de palo" which are sold as curiosities in Mexico and Guatemala. These represent placenta-like host malformations from which the parasite has fallen away and form an intricate, fluted pattern of a radial arrangement (Kuijt, 1964).

### STRUTHANTHUS Martius

#### Nomen Conservandum Propositum

Shrubs, epiphyte-like hemiparasites of trees, often unisexual, glabrous, stems erect, pendent, clambering, or climbing by means of twisted (grasping) petioles, twining terminal shoots, or attaching roots; epicortical roots from base and stems. Leaves opposite or subopposite (often on the same stem), articulate at the base (the leaves of new young shoots often very different from the leaves of mature flowering stems), lamina margins usually decurrent on the petiole and usually with differentiated tissue on the edge, venation pinnate. Inflorescences 1 to several (9) in the axils of leaves, ours with an unbranched axis of sessile or pedunculate triads (monads in *S. panamensis*) to produce spicate or racemose panicles, peduncle of the triads associated with bracts that are usually caducous, central flower of the triad usually sessile, the laterals often becoming short pedicellate, floral bracts very small and usually caducous, the flowers generally small (less than 10 mm) with denticulate or entire calyculus and free petals; male flowers with the distal part of the bud expanded to include the anthers, petals valvate in bud, usually 6, becoming reflexed at anthesis, stamens epipetalous and slightly dimorphic, the anthers borne at 2 superposed levels on adjacent petals, filaments usually very short, anthers dehiscing longitudinally, pollen said to be of 2 types (functional and rugose, sterile and smooth), nonfunctional style slender, stigma absent; female flowers often smaller than the male, buds narrowed toward the apex, the petals not usually becoming reflexed, epipetalous staminodes usually small and slender, style simple and equaling the petals, with longitudinal ridges, stigma often capitate. Fruit a berry, the calyculus not developing, rounded at the apex, seed with white endosperm.

*Struthanthus* is a neotropical genus of probably more than 60 species. The genus has never been monographed nor has its relationship with closely similar genera been properly defined. The recent segregation of *Cladocolea* (Kuijt, 1975) has resolved some issues, but the problem of distinguishing *Phthirusa* remains. The species of *Struthanthus* also present problems; e.g., they are often not easily identifiable. This is partly due to similarity of flowers and unisexuality of the plants, but the variation of floral and vegetative characters within each species adds to the problem. An extreme example is seen in young plants of *S. leptostachyus*, the leaves of which may be up to 11 cm long and 0.5 cm wide. These long, linear, fleshy, pendent leaves are gradually replaced by the broad thin organs of the mature plant (Kuijt, 1964).



KEY TO THE SPECIES OF *Struthanthus*

- 1a Inflorescences at first enclosed by 4 ranks of decussate imbricate bud scales, these broadly triangular and scarious, mostly deciduous; flowers bisexual or functionally unisexual and similar in form in the 2 sexes. .... 2a
- 1b Inflorescences not at first enclosed in an imbricate series of decussate bud scales; flowers in triads or monads with abaxial bracts that may persist or be caducous, but not thin and scarious; flowers unisexual with the male flower buds distinctly broader near the apex and enclosing the functional anthers, the female flower buds with a narrow tubular perianth and with the nonfunctional anthers small or undeveloped. .... 3a
- 2a Flowers in monads, subtended by 3 persisting and conspicuous bracts on a short thick peduncle; leaves to ca. 10 cm long, often short-acuminate; rare plants known only from ca. 1,800 m elevation in Chiriquí province, Panama  
*S. panamensis*
- 2b Flowers usually in triads (groups of 3), sessile on the axis of the inflorescence, the subtending bracts quickly deciduous; leaves to 20 cm long (in ours); evergreen and partly deciduous vegetation, 0–2,000 m. .... *S. leptostachyus*
- 3a Inflorescence very short, rarely more than 2 cm long, rarely with more than 3 pairs of triads; laminae usually less than 8 cm long and often rounded or blunt at the apex; stems terete and often becoming reddish lenticellate, 0–2,100 m. .... *S. oerstedii*
- 3b Inflorescences usually more than 2 cm long, rarely with less than 4 pairs of triads. .... 4a
- 4a Inflorescences with conspicuous (3 mm) persisting bracts beneath the triads and obscuring the base of the ovaries; apex of the ovary (edge of the calyculus) 2–2.7 mm broad, anthers 1.2–1.6 mm long on short filaments; fruit becoming 10 mm long and 6 mm thick; laminae rounded or emarginate apically and usually less than 7 cm long; 1,200–2,000 m in western Panama. .... *S. rotundatus*
- 4b Inflorescences with the bracts at the apex of the peduncle less than 3 mm long or deciduous before the flowers open; flattened apex of the ovary less than 2 mm broad. .... 5a
- 5a Leaves often grasping stems with twisting petioles, laminae usually less than 8 cm long, usually rounded apically; male perianth 4.5–6 mm long, anthers 0.8–1.3 mm long and usually sessile; fruit becoming 10 mm long, cylindrical and bluish on lenticellate peduncles; 0–1,200 m and widespread. .... *S. orbicularis*
- 5b Leaves lacking twisting petioles, but the leaves sometimes curved and the stem sometimes twining; fruit usually less than 7 mm long and the fruiting peduncle without lenticels. .... 6a
- 6a Some stems twining and with the leaves early deciduous, laminae attenuate at the base and often obovate, rounded to short-acuminate at the apex, the secondary veins prominent on dried laminae; flowers sessile or subsessile, male perianth 4.5–5.5 mm long, anthers 1–1.2 mm long; female perianth 2.5–3.5 mm long; fruit becoming pedunculate, berries orange-red and becoming constricted around the middle, the central berry (of a triad) often projecting obliquely downward/backward (toward the inflorescence base); (100) 500–1,800 m. .... *S. costaricensis*
- 6b Tips of some stems not quickly losing their leaves and twining; fruit not constricted centrally or projecting backward; leaves often relatively thin and drying stiffly chartaceous, often with acuminate apices. .... 7a
- 7a Laminae narrowly ovate-elliptic to lanceolate, long-acuminate at the apex, secondary veins strongly ascending and usually drying dark and prominent; male perianth ca. 4.5 mm long with anthers 1.2 mm long; female perianth 3–4 mm long; ovary ca. 1 mm thick; 0–500 m elevation. .... *S. woodsonii*
- 7b Only the smaller leaves lanceolate, the venation often obscure; plants of higher altitudes, 1,000–3,000 m. .... 8a
- 8a Stems usually terete, laminae acute to short-acuminate; male flowers 6–8 mm long, anthers 1–1.6 mm long; female flowers 4–6 mm long; fruit to 7 mm long; areas around Volcan Irazu and Volcan Turrialba. .... *S. marginatus*
- 8b Stems usually 4-angled, laminae often long-acuminate; male flowers 4–5 mm long, anthers ca. 0.8 mm long; female flowers 3–4.5 mm long; fruit to 5 mm long (dry); Central Volcanic Highlands to the Cordillera de Talamanca. .... *S. quercicola*

***Struthanthus costaricensis*** Standley, Publ. Field Columbian Mus., Bot. Ser. 4:202, 1929. Figure 7.

Shrubs, branch parasites often forming pendent masses, tips of stems often twining about supporting branches, leafy internodes 2–12 cm long, 1.2–5 (8) mm thick, terete or obscurely angled (flattened) at first, becoming terete with small lenticels and longitudinally striate, gray; epicortical roots often produced on stems contacting other objects. Leaves opposite, subopposite, or alternate, recurved when young but not prehensile, often early deciduous when near the apex of a twining stem, articulate at the base, petioles 10–20 mm long, somewhat vaginate near the base with winglike margins continuous with the laminae margins; laminae 3–9 (14) cm long, 2–5 (9) cm broad, broadly elliptic to obovate or spatulate (rarely suborbicular), obtuse to short-acuminate (rarely rounded) at the apex, gradually tapering to the attenuate base or occasionally obtuse to truncate, margin entire and slightly revolute (dry), decurrent on the petiole, the laminae drying subcoriaceous to coriaceous, venation pinnate with 4–7 pairs of major secondary veins arising mostly from the lower half of the midvein and ascending at angles of ca. 45°. Inflorescences 1–3 (occasionally to 9 in the males) in the axils of leaves, the spicate panicles 2–6 cm long, triads sessile or subsessile, alternate to opposite and 3–15 mm distant along the slender (0.5–1.7 mm) ridged rachis, ca. 8 triads on female inflorescences, more in the male, flowers sessile or the lateral females with very short pedicels, floral bracts minute and caducous, male flowers 5–7 mm long, ovary and calyculus 1–1.5 mm long, narrowed at the base and flared at the calyculus to 2 mm broad, perianth ca. 4 mm long before anthesis, becoming reflexed, stamens with short (0.5 mm) filaments, anthers 0.8–1.2 mm long; female flowers ca. 4–5 mm long, petals ca. 3 mm long with minute (0.3 mm) slender epipetalous stamens, style ca. 3 mm long with capitate stigma. Fruit ellipsoid to cylindrical, becoming ca. 5 mm long and 3 mm thick, slightly constricted in the middle, red to orange, the lateral fruit of a triad on pedicels becoming up to 3 mm long.

Epiphyte-like hemiparasites of moist evergreen or partly deciduous forest formations between 500 and 1,800 m elevation on both the Caribbean and Pacific slopes of Costa Rica; flowering collections have been made between November and July. The species is found only in Costa Rica and western Panama.

*Struthanthus costaricensis* is recognized by the presence of stems with small-leaved twining tips, subopposite leaves on terete stems, stiff laminae with attenuate base (decurrent on the petioles), and relatively small red-orange fruit slightly constricted in the middle. This species is closely related to *S. orbicularis*, but that species lacks the twining stems and has prehensile (grasping) petioles, angled stems, and larger bluish fruit on lenticellate pedicels.

***Struthanthus leptostachyus*** (H.B.K.) G. Don, Gen. Hist. Dichlam. Pl. 3:411. 1834. *Loranthus leptostachyus* H.B.K., Nov. Gen. Sp. 3:440. 1818. *Peristethium leptostachyum* (H.B.K.) Van Tieghem, Bull. Soc. Bot. France 42:175. 1895. *Phthirusa pittieri* Krause, Feddes Repert. 15:441–442. 1919. *Struthanthus polystachyus* sensu auctores. Figure 6.

Large shrubs, with horizontal or scandent branches over 2 m long, leafy internodes 2–9 cm long, 1.5–8 mm thick, raised brownish lenticels often present on older and thicker stems; epicortical roots produced from the base and from the stems, those from the base occasionally becoming over 30 cm long. Leaves opposite or subopposite (occasionally a few alternate leaves present), articulate at the base, petioles 10–25 mm long, 1.4–4.5 mm thick, slightly sulcate above with adaxial ridges continuous with the lamina margins; laminae 5–16 (20) cm long, 3–8 (12) cm broad, broadly ovate-lanceolate to ovate, elliptic-ovate, or elliptic-oblong, usually gradually narrowed to the acuminate apex, rounded and subtruncate to obtuse at the base, margins entire and becoming revolute, tissue of the edge slightly differentiated and smooth, the laminae drying stiffly chartaceous, glabrous and smooth, venation pinnate with 5–10 pairs of major secondary veins arising throughout the length of the midvein, secondary veins slightly raised above and often obscure beneath. Inflorescences solitary or 2–4 in the axils of leaves or fallen leaves, unisexual, at first

enclosed in pale scarious keeled bracts (scales) ca. 3 mm long, these caducous with expansion of the spike, the spikes becoming 2–8 cm long, with ca. 14–18 opposite triads of flowers or with solitary flowers near the apex of the spike, triads subtended by the bract-(scale-) scar, rachis ca. 1 mm thick and longitudinally striate when dry, glabrous but developing lenticels in fruit; flowers 4–6 mm long, unisexual, the female somewhat more slender than the male, ovary 1–1.5 mm long with thin subentire calyculus, perianth parts 3–4 mm long, male flowers with anthers sessile on the perianth, subequally attached, 1 mm long. Fruit becoming 6 mm long and 4 mm thick, truncated at base and apex or somewhat ellipsoid.

Epiphyte-like hemiparasites of wet evergreen or partly deciduous forest formations from sea level to 2,000 m elevation on both the Caribbean and Pacific slopes; probably flowering throughout the year, but not collected in September, October, and November in our area. The northernmost collection of the species comes from near Tilaran, Guanacaste, while the southernmost are reported to be from Peru.

*Struthanthus leptostachyus* is recognized by its large size (for a parasite), epicortical roots arising from various areas on the stems, leaves with acuminate apices, small unisexual yellow flowers in sessile triads, and the spikes at first enclosed in imbricate bracts resembling bud scales. These scales and the rather large leaves distinguish this species from most of our other species of *Struthanthus*. This species resembles *Phthirusa pyrifolia* in a superficial way.

***Struthanthus marginatus* (Desr.) Blume**, in Schult., Syst. Veg. 7, pt. 2:1731. 1830. *Loranthus marginatus* Desr., in Lam., Encycl. 3:596. 1789. Figure 7.

Shrubs or climbers, branch parasites, often covering the crowns of small trees, leafy internodes 2–5 cm long, 1.3–3.5 (5) mm thick, pale brown and smooth, becoming grayish with small round lenticels, longitudinally striate (dry) but terete; clasping roots produced in groups or series on stems and often ramifying. Leaves opposite, subopposite, or occasionally alternate, petioles 3–5 mm long, ca. 1.3 mm thick, somewhat sulcate above or slightly winged; laminae 4–8 (12) cm long, 1–4 (7) cm broad, narrowly elliptic-oblong to broadly elliptic, ovate, or lanceolate, tapering gradually to an acuminate to acute apex (rarely rounded), obtuse to acute at the base with the margins decurrent on the petiole, margin thin and becoming slightly revolute, laminae drying stiffly chartaceous and often brittle, smooth and glabrous, the 3–7 pairs of major secondary veins often difficult to distinguish from the tertiaries, the tertiary veins obscure or slightly raised on the dried surfaces. Inflorescences solitary or 2–3 in the axils of leaves, racemose panicles 2–7 cm long, the 8–14 triads evenly spaced in usually opposite or subopposite pairs along the slender (0.7–1.4 mm) rachis, peduncles of the triads 1–3 (5) mm long with a small (3 mm) caducous bract at the apex, triads with the central flower sessile and the lateral flowers sessile or very short- (0.3–1 mm) pedicellate; male flowers 6–8 mm long, ovary and calyculus 1.5–2 mm long, perianth cream color, 5–6 mm long, becoming reflexed, stamens with very short filaments, anthers 1–1.6 mm long and almost versatile; female flowers 4–6 mm long, the perianth ca. 3.5–4 mm long, narrow, yellow-green, staminodes with reduced anthers ca. 0.6 mm long, style 3.3–4 mm long with a capitate stigma. Fruit ovoid, becoming 7 mm long and 5 mm in diameter, the central fruit of a triad sessile, the laterals usually pedicellate.

Epiphyte-like hemiparasites of moist evergreen forest formations between about 1,000 and 3,000 m elevation; flowering collections have been made between February and July. The species has been collected only from around the eastern edge of the Meseta Central and the adjacent volcanoes (Irazu and Turrialba) and in the Chiriquí Highlands (Panama) in our area. The species is also known from Brazil (but see below).

*Struthanthus marginatus* is distinguished by its (sub)opposite leaves on smooth often climbing stems, thin laminae that often have short-acuminate apices, evenly

spaced short-pedunculate triads with sessile central flowers, and the lack of apparent bracts beneath the flowers or at the apex of the peduncle in flowering and fruiting stages. The restriction to the eastern edge of the central volcanic area is a further unusual characteristic. Specimens of *S. quercicola* have frequently been placed under this name, and the two species are similar in appearance. They seem to share the same habitats, and yet, if present collections are truly representative, they are not found in the same localities. It may be that *S. marginatus* is restricted to the premontane and lower montane wet forests, while *S. quercicola* is found in the moister rain forest life zones as defined by Tosi & Holdridge.

There is some question regarding the use of the name *Struthanthus marginatus* in our area. A photograph of the type and material from eastern Brazil, where the type was collected, differ from our specimens in having smaller (0.5 mm) anthers more versatile on filaments which average about 1.5 mm long (dry). Both male and female flowers of the Brazilian material are smaller than their Central American counterparts. However, it seems best to let current usage stand until this very difficult genus receives monographic treatment.

***Struthanthus oerstedii*** (Oliv.) Standley & Calderon, Lista Prelim. Pl. Salvad. 74. 1925. *Loranthus oerstedii* Oliver, Vidensk. Meddel. Dansk Naturhist. Foren. Kjoebenhavn 1864:171. 1865. Figure 7.

Shrubs, unisexual, branches not usually over 1 m long, leafy internodes 0.4–5 (8) cm long, 1.4–4 mm thick, terete, usually becoming rough and reddish brown with many small (0.1–0.2 mm) lenticels; epicortical roots developed from the stem and numerous. Leaves opposite, subopposite, or occasionally alternate, articulate at the base, petioles 2–5 mm long, ca. 1.5 mm broad, slightly sulcate with edges continuous with the lamina margins; laminae 1.5–8 (10) cm long, 1–3 (5) cm broad, elliptic to slightly ovate or rhombic, tapering gradually or abruptly to an acute, obtuse or rounded (rarely acuminate) apex, obtuse to attenuate at the base, margin entire and revolute on drying, decurrent on the petiole, laminae drying very stiffly chartaceous to subcoriaceous, smooth and glabrous, venation pinnate with 2–6 pairs of major secondary veins difficult to distinguish from the tertiaries, the proximal secondaries usually arcuate-ascending, tertiary veins often raised above. Inflorescences 1 to several in a leaf axil, 1–2 cm long, usually with ca. 4 triads, primary peduncle 0–5 mm long, peduncles of the triads 1–5 mm long, bracts subtending the flowers ca. 1 mm long; flowers sessile, unisexual, the male 4–6 mm long, petals slightly dimorphic and reflexed at anthesis, ca. 4 mm long, anthers subsessile, ca. 0.7 mm long, yellow; female flowers ca. 4–5 mm long and narrowed to the apex before anthesis, staminodia fused with the petals, stigma undifferentiated. Fruit ovoid, becoming ca. 5 mm long, green (immature?) truncated at the apex and with a thickened area interior to the calyx, bracts persisting but small.

Epiphyte-like hemiparasites of deciduous and evergreen forest formations between sea level and 2,100 m elevation; flowering collections have been made between June and September and in January and February. The species appears to be endemic to the area between central Nicaragua and central Costa Rica, but it has not been found below 500 m elevation on the Caribbean slope.

*Struthanthus oerstedii* is recognized by the reddish brown lenticellate stems, small elliptic leaves blunt at the apex, and the very small inflorescences with sessile flowers. The southernmost collections of the species come from La Suisa (Cartago) on the Caribbean slope and from Puntarenas on the Pacific slope. An unusual collection from the Pacific coast near Nicaragua (Howell 10243) was segregated by Kuijt as species number 38 in his study of 1964. Comparison with material from Nicaragua, where Oersted collected the type, suggests that this specimen falls within the pattern of variation encompassed by *S. oerstedii*.



***Struthanthus orbicularis*** (H.B.K.) Bl., in Schult., Syst. Veg. 7, pt. 2:1731. 1830. *Loranthus orbicularis* H.B.K., Nov. Gen. & Sp. 3:434. 1820. *Loranthus chordocladus* Oliver, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1864:173. 1865. *S. chordocladus* (Oliv.) Eichl., Fl. Brasil. 5, pt. 2:70. 1868. *S. belizensis* Lundell, Lloydia 2:83. 1939. Figure 7.

Scandent shrubs, often climbing over small trees or with pendent stems to 2 m long, leafy internodes 3–9 cm long, 1.5–5 mm thick, quadrangular or flattened with 2 longitudinal ridges, smooth and striate (dry); epicortical roots from base and stems. Leaves opposite or subopposite (occasionally alternate), at first lanceolate and recurved and functioning to climb over adjacent vegetation, the later leaves as described, articulate at the base, petioles 4–12 mm long, ca. 1.5 mm broad with lateral ridges continuous with the lamina margins; laminae 2.5–6 (8) cm long, 1.2–3 (6) cm broad, obovate to suborbicular or elliptic, bluntly obtuse to rounded at the apex with apiculate to emarginate tip, obtuse to rounded at the base, margin entire, becoming slightly revolute, the edge thin and smooth, decurrent on the petiole, the laminae drying stiffly chartaceous to subcoriaceous, venation pinnate with 3–7 pairs of major secondary veins arising throughout the length of the midvein. Inflorescence solitary in axils of leaves (occasionally fallen leaves), 3–16 cm long, unbranched spicate or racemose panicles, the triads 3–11 mm distant on the smooth, striate (dry) and ridged rachis 1–3 mm thick, peduncles of the triads 0–2 mm long, subtended by caducous bracts 3–6 mm long (rarely seen on dry specimens), pedicels of the flowers 0–1 mm long at anthesis, not expanded at the apex beneath the ovary (the floral bracts not apparent); male flowers 6–8 mm long, yellowish, ovary ca. 1.7 mm long with slightly flared calyculus 0.5 mm long and 1–1.8 mm broad at the apex, perianth 5–6 mm long, anthers subsessile or on very short filaments at 2 different levels on alternating petals, anthers 0.8–1.5 mm long, 1 mm broad, the connective apiculate; female flowers more tubular, 4–6 mm long, staminodes reduced to ridges on the perianth, stigma subcapitate. Fruit borne on pedicels becoming 8 mm long and 2 mm thick with conspicuous (0.7 mm) brownish lenticels, fruit becoming 10–13 mm long, 6–8 mm thick, truncated at the apex, ellipsoid to cylindrical, purple to blue.

Epiphyte-like hemiparasitic climbers in evergreen or partly deciduous forest formations from sea level to 1,200 m elevation; collected with flowers from October to June in Costa Rica. The species ranges from southern Mexico to Brazil and Peru.

*Struthanthus orbicularis* is distinguished by its usually opposite rounded leaves on smooth climbing or trailing stems, spicate inflorescences with subsessile triads of flowers that develop expanded lenticellate pedicels in fruit, and moist lower elevation habitats. The species is apparently rare on the Caribbean slope of Costa Rica.

***Struthanthus panamensis*** (Riz.) Barlow & Wiens, Brittonia 25:39. 1973. *Phrygilanthus panamensis* Rizzini, Ann. Missouri Bot. Gard. 47:270. 1961. Figure 6.

Shrubs or clambering branch parasites, apparently bisexual, leafy internodes 1–6 cm long, 1–4 mm thick, terete or slightly ridged in early stages, smooth and grayish. Leaves opposite or subopposite, articulate at the base, petioles 7–22 mm long, 1–2 mm thick, narrowly sulcate above with thin adaxial margins continuous with the lamina margins; laminae 3.5–10 cm long, 1.5–6 cm broad, ovate to ovate-oblong, acute to acuminate or caudate-acuminate at the apex, the tip often elongate, truncate to obtuse or rounded at the base, margins entire and slightly revolute (dry), the edge differentiated and smooth, the laminae drying stiffly chartaceous to subcoriaceous, venation pinnate, the 3–7 pairs of major secondary veins usually obscure on both surfaces. Inflorescences 1–3 in the axils of leaves, at first subtended by 4–6 pairs of stiff decussate imbricate bracts resembling bud scales, racemose, 1–3 (4) cm long with flowers borne on pedicels bracteate at their apex, pedicels 1–2 mm long and 0.5–1 mm broad, the pedicelled flowers (opposite monads) 2–6 mm distant along the thick (1 mm) strongly 4-angled rachis, the abaxial bract decurrent on the peduncle with free apex ca. 2 mm long, lateral bracts ca. 1 mm long, persisting; the



flowers and bracts drying black, flower buds becoming 8–12 mm long, 2 mm thick distally but narrowed to an acute and often slightly curved apex, yellow, calyculus minute and entire, petals 6 and narrowly acute at the apex, yellow-green, anthers sessile at 2 different levels on adjacent petals, ca. 1.2–1.8 mm long, apiculate, style ca. 5 mm long, stigma only slightly thickened. Fruit apparently globose, 5–8 mm long and equally thick, yellow, apex with a thick central disklike area within the thin calyculus, bracts and bractlets persisting in fruit.

Epiphyte-like hemiparasites of evergreen montane (lower montane rain) forest formations between 1,800 and 2,200 m elevation in western Panama. The species is known only from Chiriqui, Panama. Flowers were collected in March (Davidson, 431, the type, and 392) and May (Luteyn 3786), and mature fruit, in January (Wilbur & Teeri 1310a).

*Struthanthus panamensis* is recognized by its stiff opposite leaves on terete stems, laminae often ovate and caudate-acuminate at the tip, short racemose inflorescences, and single flowers on short stalks with one larger (abaxial) bract and two smaller lateral bracts that persist in fruit. The flowers appear to be bisexual, but may be functionally unisexual and male in the type, the only flowering material seen. The very narrow petal tips are unusual among our species of *Struthanthus*.

The correct genus for this species is in doubt, and its placement in *Struthanthus* should be considered provisional. See the discussion by Kuijt in Ann. Missouri Bot. Gard. 65:761, 1978. The term pedicel is used in this description for stalks bearing a single flower or monad.

***Struthanthus quercicola*** (S. & C.) Blume, in Schult., Syst. Veg. 7:1731. 1830. *Loranthus quercicola* Schlecht. & Cham., Linnaea 5:173. 1830. *L. cansjeraefolius* Oliver, Vidensk. Meddel. Dansk Naturhist. Foren. Kjoebenhavn 1864:173. 1865, e descr. et photo. *Struthanthus cansjeraefolius* (Oliv.) Eichler, in Martius, Fl. Brasil. 5, pt. 2:87. 1868. Figure 7.

Shrubs or with climbing or pendent stems, to over 3 m long, leafy internodes 2–12 cm long, 1–4 mm thick, smooth, strongly 4-angled or with 4 longitudinal ridges but becoming terete, pale gray; epicortical roots common on stems. Leaves opposite, subopposite, or occasionally alternate, articulate at the base, petioles 3–8 (11) mm long, 1–2 mm broad, slightly sulcate or flattened and continuous with the lamina margins; laminae (3.5) 5–10 (13) cm long, (1) 2–5 (7) cm broad, ovate to elliptic-ovate, gradually tapering to the cuspidate or long-acuminate apex, obtuse at the base with the margin decurrent on the petiole, margin entire and becoming slightly revolute, the laminae drying very stiffly chartaceous, smooth and glabrous, venation pinnate with 3–6 pairs of major secondary veins often difficult to distinguish from the tertiary veins, the tertiaries usually slightly raised above. Inflorescences usually solitary (3–5) in the axils of leaves, racemose panicles 2–6 cm long with 5–12 triads 3–10 mm distant on the slender (0.7–1.5 mm) rachis, the rachis usually with 4 longitudinal ridges, peduncles of the triads (1) 2–3 (6) mm long, bracts beneath the flowers 0.5–2 mm long, deciduous or occasionally persisting; the central flowers sessile and the laterals subsessile or very short pedicellate, male flowers 4–5 mm long, ovary and the very short calyculus ca. 1 mm long, perianth 3–4 mm long, becoming reflexed, stamens with very short filaments, anthers ca. 0.8 mm long; female flowers 3.2–4.5 mm long, perianth 2–3 mm long and not becoming reflexed, staminodes small with very slender nonfunctional anthers, style 2–3 mm long, stigma capitate and faintly 3-lobed. Fruit becoming ca. 5 mm long and 4–5 mm thick, ellipsoid to ovoid, bright orange.

Epiphyte-like hemiparasites of evergreen montane forest formations of the Cordillera de Tilaran, Central Volcanic Highlands, and the Cordillera de Talamanca between (600) 1,200 and 2,300 (2,800) m elevation; flowering material has been collected from December to June. The species, as here interpreted, ranges from Jalapa, Mexico, to western Panama.

*Struthanthus quercicola* is distinguished by its opposite and subopposite leaves on smooth stems, relatively thin laminae with long-acuminate apices, evenly spaced triads on slender peduncles, inconspicuous floral bracts, and orange fruit. *Struthanthus quercicola* has been collected along the Caribbean side of the Central Highlands (Zarero, Volcan Poas, Volcan Barba, La Palma, to the vicinity of Cartago) and along the Talamanca mountains to above San Isidro del General. This distribution differs from that of *S. marginatus* which is found on the slopes of Volcan Irazu and Volcan Turrialba. The two distributions overlap in the area between San Jose and Cartago, and yet there are no collections of the two species from the same locality, such as Tres Rios or the campus of the university. Material of this species has usually been identified as *S. marginatus*; see the discussion under *S. marginatus*. *Struthanthus papillosus* Standl. & Steyerf. of Guatemala may prove to be this species.

Included here are specimens from between 600 and about 1,100 m altitude on the Pacific slope of Costa Rica that were segregated as a separate entity (No. 37) by Kuijt in 1964. These plants tend to have more narrow leaves, shorter inflorescences, and longer peduncles, and the little bracts subtending the flowers are less often persisting. While they do appear quite different from most of the *S. quercicola* material collected from the Central Highlands, they do not appear as different when compared with material from Chiriqui, Panama. This group of specimens ranges from the area of San Ramon (*Brenes* 1704 and 22889) to the highlands bounding the Pacific side of the General Valley (*Allen* 5891, *Burger & Baker* 10105 and 10108, *Kuijt* 2446), all between about 800 and 1,100 m elevation. A very unusual specimen (*Skutch* 3954) with small (5 by 1.5 cm) lanceolate laminae and very short (2 cm) inflorescences from the area of El General at 610 m altitude is also included here.

Kuijt (1978) has recently identified a number of Panamanian collections as *Struthanthus* aff. *dichotrianthus* Eichler. These have a leaf form and habit very similar to those of *S. quercicola*, but they differ in having longer and narrower leaves and much shorter inflorescences with fewer triads. These characteristics have not been seen in Costa Rican collections.

***Struthanthus rotundatus* Rizzini, Rev. Brasil. Biol. 10:401. 1950. Figure 7.**

Climbing branch parasitic shrubs, leafy internodes (2) 4–18 cm long, (1.5) 2–6 mm thick, smooth but with longitudinal ridges and somewhat 4-angled, soon becoming terete; epicortical roots few from the internodes, more often from the nodes. Leaves opposite or subopposite, articulate at the base, petioles 5–20 (28) mm long, 1.1–2 mm thick, often somewhat sulcate above with adaxial ridges continuous with the lamina margins; laminae 2.5–7 cm long, 2–6 cm broad, broadly obovate to suborbicular or broadly oblong, usually rounded and emarginate at the apex, obtuse to subtruncate at the base, margin entire and decurrent on the petiole, often undulate and slightly revolute when dry, the laminae drying subcoriaceous to stiffly chartaceous and brittle, smooth and glabrous, venation pinnate with 4–8 pairs of major secondary veins arising from throughout the length of the midvein, ascending at angles of ca. 45°. Inflorescences solitary in the axils of leaves or fallen leaves, 5–15 cm long, unbranched racemose panicles with opposite or subopposite triads 3–12 mm distant on the rachis, rachis 1.5–2 mm thick (dry) and with longitudinal ridges, peduncles of the triads 1–3 mm long with the subtending (abaxial) bract adnate and persisting, these bracts ca. 6 mm long from base of the peduncles to the acute or obtuse tip, apparently fleshy, the sessile flowers subtended by shorter (2–3 mm) floral bracts similar to the larger bract in texture; male flowers ca. 8 mm long, ovary and calyculus 2 mm long and 2–2.7 mm in diameter distally, perianth parts (petals) ca. 6 mm long, stamens with very short (0.5 mm) filaments, borne at 2 levels on adjacent perianth parts, anthers 1–1.7 mm long, connective apiculate; female flowers similar in size and form to the male,

calyculus subentire and thin, staminodes with reduced (0.5 mm) anthers on very short filaments, style ca. 5 mm long with thickened stigma. Fruit ca. 10 mm long and 6 mm thick, ellipsoid or somewhat truncated at base and apex, becoming red, borne on thick (2 mm) peduncles to 5 mm long with occasional round brownish lenticels, bracts persisting at the base of the sessile fruit.

Epiphyte-like hemiparasitic climbing plants of the wet montane forests of westernmost Panama between 1,200 and 2,000 m elevation; probably flowering throughout the year, but collected with flowers only in January, March, June, July, and September. The species is known only from western Panama and Brazil (fide Rizzini).

*Struthanthus rotundatus* is distinguished by its opposite rounded leaves on smooth climbing stems often slightly quadrangular in cross section, racemose inflorescences with sessile flowers in bracteate and pedunculate triads, the bracts adnate to and persisting on the apex of the peduncles, and the restricted higher elevation habitat. The anthers and staminodes with very short filaments further distinguish this species from the very similar *S. orbicularis*. While not yet recorded from Costa Rica, this species is to be expected in the montane forests adjacent to Panama. *Struthanthus macrostachyus* Lundell from Chiapas, Mexico, appears to be a close relative of *S. rotundatus*.

***Struthanthus woodsonii* Cufodontis, Arch. Bot. Sist. 10:31. 1934. Figure 6.**

Twining shrubs with slender stems, leafy internodes (2) 4–12 cm long, 1–4 mm thick, terete, smooth and usually drying dark; epicortical roots not usually found on flowering stems. Leaves opposite, subopposite, or alternate, articulate at the base, petioles 2–7 mm long, 0.6–1 mm thick, sulcate above with the adaxial margins continuous with the lamina margins; laminae (2.5) 4–10 cm long, (0.6) 1.5–4 cm broad, very narrowly ovate to lanceolate or narrowly elliptic-ovate, gradually tapering to the acute to long-acuminate apex, acute to obtuse at the base, margin entire, the laminae drying stiffly chartaceous, the 2–4 pairs of major secondary veins usually arising from the proximal half of the midvein and strongly ascending, occasionally with the basal pair of secondaries very prominent and the leaf appearing trinerved, secondary and tertiary veins usually slightly raised on both surfaces when dry. Inflorescences 1 or 2 in the axils of leaves or fallen leaves, 2–6 cm long and becoming 10 cm long in fruit, the male with sessile or subsessile triads and the inflorescences spicate, the female becoming racemose panicles, the 10–16 triads 3–5 mm distant on the slender (1 mm) ridged rachis, peduncles of the female triads 0.5–3 mm long, ca. 0.5 mm thick, bract at the apex of the peduncle persisting or deciduous; male flowers 5–6 mm long, ovary narrowed at the base and expanded at the minutely denticulate or erose distal margin of the calyculus, anthers subsessile, 1–1.4 mm long and apiculate; female flowers ca. 4 mm long, ovary only slightly expanded distally, with the calyculus obscurely denticulate (erose), staminodes minute (0.2 mm), style ca. 3 mm long, stigma capitate. Fruit ca. 5 mm long and 3 mm thick, cylindrical or ellipsoid, slightly constricted around the middle, orange, the triads borne on peduncles to 8 mm long, the lateral fruits of a triad on pedicels to 3 mm long and 1.5 mm thick.

Epiphyte-like hemiparasites of aerial branches in evergreen lowland forest formations between sea level and about 500 m elevation found mostly on the Caribbean side of Costa Rica; probably flowering throughout the year, but collected with flowers only in October, February, March, and May. This species appears to be endemic to the area of Costa Rica and Bocas del Toro, Panama. A single collection from the Pacific slope (*Brenes* 22889, Rio Jesus de San Ramon, Alajuela-Puntarenas) appears to be this species.

*Struthanthus woodsonii* is recognized by its slender twining stems, the distant, usually lanceolate leaves with thin laminae and prominent ascending secondary veins (when dry), the calyculus with minutely denticulate or erose margin, and usual restriction to the lowland Caribbean area.



## VISCACEAE

Small- to medium-sized shrubs, mostly with some chlorophyll and hemiparasitic, parasitic on the aerial stems of dicotyledonous trees and shrubs (in ours) or less often on gymnosperms, attaching to the host by means of a primary haustorium which often branches within the host, young stems terete, angular, or compressed, often articulate above the node, glabrous (in ours) or rarely puberulent, the plants unisexual or bisexual, with foliage leaves or with all the leaves reduced to minute scale leaves, paired opposing scale leaves present on the inflorescences (and often called bracts), on lateral branches above branching nodes, and on percurrent stems in leafy species or defining all the nodes in leafless (squamate) species; stipules absent, paired lateral prophylls occasionally persisting above the base of lateral branches, epicortical roots absent. Leaves present or all reduced to scale leaves (squamate), opposite and decussate in ours, the foliage leaves in leaf-bearing species usually articulate at the base, simple and entire, usually thick and drying stiff or brittle, venation palmate to pinnate, glabrous in ours; the small pairs of opposite scale leaves often united at the base across the stem, generally less than 5 mm long. Inflorescence basically a spike, borne in the axils of leaves or scale leaves, rarely terminal, not ensheathed by deciduous scale leaves in early stages, bisexual or unisexual, with the male and female flowers in a variety of arrangements, the spikes composed of internodes defined by small paired scale leaves (bracts), the lower (proximal) internode(s) sterile and functioning as a peduncle, the flowers arising individually from depressions in the rachis of the fertile internodes, arranged in longitudinal ranks or other configurations on the rachis; the flowers very small and unisexual, the same color as the stems in ours, perianth of a single whorl, a calyculus absent, the perianth united with the inferior ovary beneath and usually 3-parted or 3-lobed distally, valvate in bud; male flowers with the stamens equal in number and opposite the perianth parts, stamens often borne on the perianth, on short filaments or sessile, anthers 1- or 2-thecous in ours, opening by pores or irregular slits, pollen mostly spherical; a style-like pistillode present or absent; female flowers without staminodes, ovary inferior with single locule, style and stigma 1, ovules not differentiated. Fruit a fleshy 1-seeded berry, seed solitary and surrounded by viscous tissue, endosperm with chlorophyll.

A family of about 11 genera and several hundred species; most diversified in tropical areas, but extending into milder parts of the temperate zone. *Dendrophthora* and *Phoradendron* are the New World counterparts of *Viscum* which is indigenous to Africa and parts of Europe and Asia. The epiphyte-like habit, parasitic attachment to aerial parts of trees and shrubs, stiff opposite leaves or absence of foliage leaves, and minute flowers arising from depressions in spikelike inflorescences distinguish these plants from virtually all other Costa Rican families. Only *Oryctanthus* of the Loranthaceae (s.s.) is easily mistaken for a genus of Viscaceae.

A discussion of inflorescence types (mentioned in some of the descriptions) can be found in Kuijt's "A study of heterophylly and inflorescence structure in *Dendrophthora* and *Phoradendron*" (Acta Bot. Neerl. 8:506-546, 1959).

## KEY TO THE GENERA OF VISCACEAE IN COSTA RICA

- 1a Anthers with a single theca (locule), the flowers in 2, or less often 4-6, longitudinal ranks on each fertile internode, the fertile rachis often somewhat flattened with the floral ranks on opposing narrower edges or the 6 ranks somewhat irregularly arranged on a terete rachis; plants lacking expanded foliage leaves (in 2 species) or with expanded foliage leaves and then lacking paired scale leaves on percurrent stems and with paired scale leaves ca. 5-10 mm above branching nodes on lateral stems; growing as high as 3,500 m, but rarely found below 1,800 m elevation ..... *Dendrophthora*
- 1b Anthers with 2 thecae (locules), the flowers usually in 4-6 longitudinal ranks on each fertile internode or rarely in broad circular areas, the fertile rachis terete or 4-angled in cross section; plants always with expanded foliage leaves, percurrent stems with or without paired scale leaves above the leaf-bearing node, lateral stems with paired scale leaves above the branching node (in ours); plants growing from sea level to ca. 3,000 m elevation ..... *Phoradendron*



## DENDROPTHORA Eichler

REFERENCES: Job Kuijt, A Revision of Dendrophthora. Wentia 6:1-145, 1961. A Revision of the Loranthaceae of Costa Rica. Bot. Jahrb. Syst. 83:250-326. 1964.

Shrubs, usually small (20-50 cm) but occasionally to 2 m tall (as in *D. ambigua*), branch parasites of a great variety of dicotyledonous (rarely gymnospermous) trees and shrubs, often densely branched and olive green or yellow-green in color, unisexual or bisexual, stems terete and usually articulate (winged, ridged, or compressed in some species), paired scale leaves often present on lateral stems above branching nodes, many species with all the leaves reduced to scale leaves (i.e., squamate); haustorial system apparently simple (lacking lateral expansion with aerial shoots), epicortical roots unknown. Leaves present or apparently absent and represented by minute paired scale leaves, opposite and decussate, foliage leaves with poorly differentiated petioles or subsessile, often articulate at the base, simple and entire, the scale leaves acute to obtuse, often united at the base across the stem, occasionally tubular. Inflorescences solitary in the axils of leaves or scale leaves or in groups forming compound inflorescences, rarely solitary and terminal (as in *D. terminalis*), unisexual or bisexual, basically a spike with 1 to several basal sterile internodes functioning as a peduncle, flowers arising from depressions in the rachis of the fertile internodes and arranged in 2-6 longitudinal ranks (series) on each internode (1-3 ranks above each bract in a variety of arrangements); flowers unisexual and very small, perianth of a single 3-parted or 3-lobed whorl (calyx), stamens sessile on the calyx-lobes, anthers 1-thecous and dehiscing by a transverse slit, female flowers with inferior unilocular ovary and single short style, stigma scarcely differentiated, ovules not differentiated. Fruit a berry, a layer of fleshy tissue and viscin surrounding the single seed; endosperm almost completely surrounding the undifferentiated embryo and bright green.

A genus of about 53 species in tropical America; especially numerous in eastern Cuba, Hispaniola, and the higher mountains from southern Mexico to the Bolivian Andes. Almost all the continental species and a great majority of the insular ones are restricted to mountainous areas.

The unilocular anther used to distinguish this genus from the closely allied *Phoradendron* is a very difficult character to ascertain in flowers that are so small. Most workers have, nevertheless, been able to work with these plants without having to examine the male flowers of each species. The complete or almost complete lack of foliage leaves immediately distinguish *D. squamigera* and *D. terminalis* from all our species of *Phoradendron*. *Dendrophthora costaricensis* looks very much like some species of *Phoradendron*, but has the male flowers terminal and opening later than the female flowers of the same internode, and the arrangement of flowers on the internodes is often quite irregular. *Dendrophthora* lacks the paired scale leaves found above percurrent stems (above nonbranching nodes) found in some species of *Phoradendron*.

- 1a Foliage leaves absent or a few pairs of leaves present near the base of the plant, almost all nodes with small scale leaves in opposing pairs; spikes axillary or terminal. . . . . 2
- 1b Foliage leaves present on the stems, small scale leaves present on inflorescences and above branching nodes; spikes only from the axils of leaves. . . . . 3
- 2a Spikes numerous and arising from the axils of scale leaves, in opposing pairs; scale leaves to 2 mm long, prophylls obscure; common plants of high montane formations, 2,400-3,400 m. . . . . *D. squamigera*
- 2b Spikes fewer, solitary and terminal on short stems; scale leaves to 5 mm long, prophylls ca. 2 mm long and persisting above the branching node; rare plants known only from around 1,700 m. . . . . *D. terminalis*
- 3a Plants to ca. 1 m in diameter, leaves without a stiff leathery margin, drying thin and yellowish; spikes solitary in leaf axils, flowers in 6 irregular ranks on each fertile internode, flowering rachis terete; common plants from (1,500) 1,800-3,300 m elevation. . . . . *D. costaricensis*
- 3b Plants to 2 m in diameter, leaves with a stiff leathery margin, drying thick and dark in color; spikes 1 or several in the leaf axils, flowers in 2 opposing ranks or up to 6

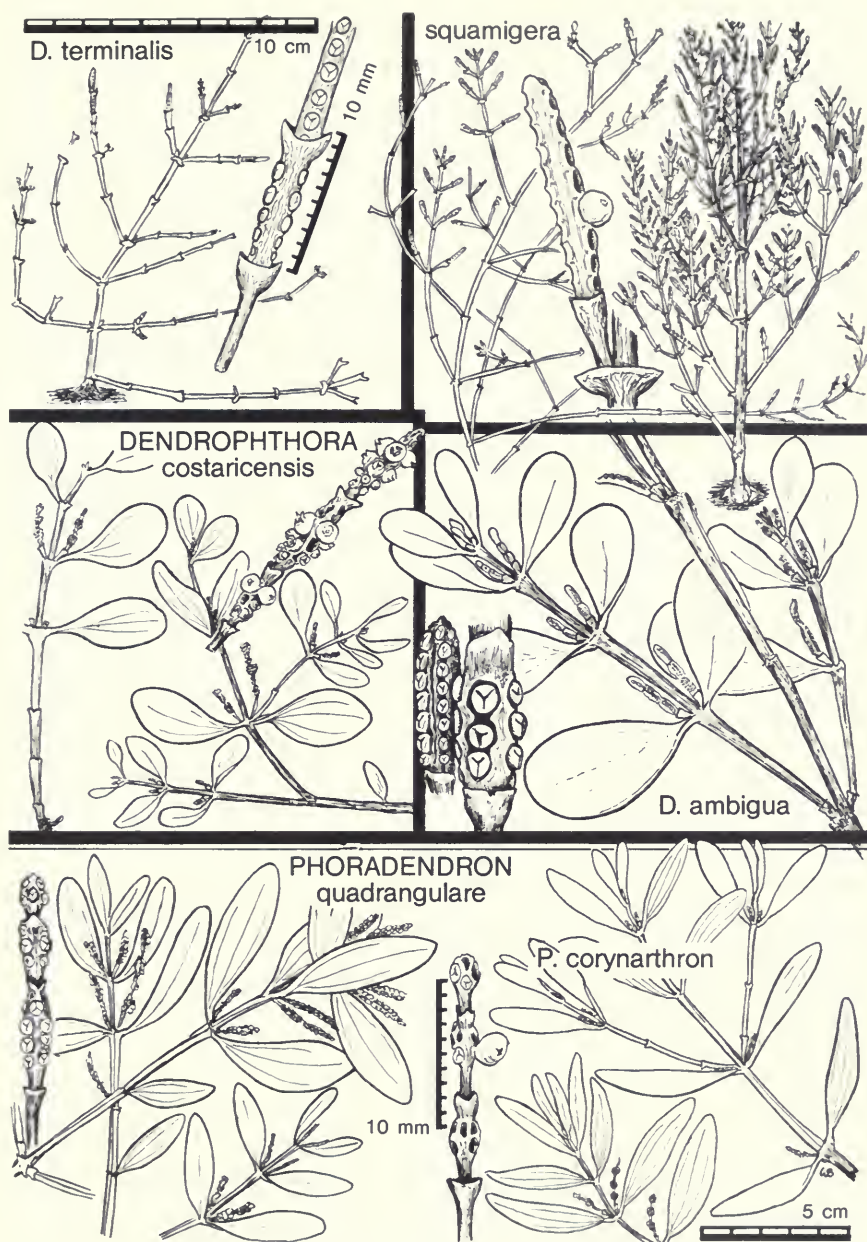


FIG. 9. Viscaceae: species of *Dendrophthora* and two species of *Phoradendron*.



FIG. 10. Viscaceae: species of *Phoradendron*, second group.





FIG. 11. Viscaceae: species of *Phoradendron*, third group.



ranks on a fertile internode, variable in the number of ranks but often with the rachis flattened and the flower ranks on the opposing edges of the rachis; rare plants probably not growing below 2,500 m. . . . . *D. ambigua*

***Dendrophthora ambigua* Kuijt, Wentia 6:29–30. 1961. Figure 9.**

Shrubs or subshrubs to 2 m in diameter, bisexual, leafy internodes 5–30 mm long, 2–6 mm thick, becoming striate and dark on drying, terete or slightly flattened beneath the nodes, branching vegetative stems with a pair of scale leaves ca. 1 cm above the branching node, the scale leaves (cataphylls) appressed to the stem in life but becoming separate in herbarium material, the node bearing the scale leaves swollen in living material. Leaves present throughout the plant, symmetrical, petioles 4–12 mm long but not clearly differentiated from the lamina, lateral ridges of the petiole continuous with the lamina margins; laminae 2–5 (7) cm long, 1.5–3 (5) cm broad, obovate to spatulate or elliptic-obovate, rounded at the apex, gradually narrowed at the base, entire and with a brown leathery margin, the laminae drying very dark and stiffly coriaceous, venation palmate, the 3–5 primary veins usually obscure. Inflorescences solitary or several in the axils of leaves, up to 9 cm long with 2 or 3 fertile internodes 2–3 cm long, arrangement of sexes and flowers very variable, both sexes may be present on the same internode or even above the same bract (in the same rank), female flowers normally in an apical position in bisexual internodes and most commonly in a single median rank (series), the fertile internodes most often with 2 opposing longitudinal ranks, but also with 2 or 3 ranks on each side above the bract (2–6 ranks or series per internode in 2A or 1B arrangements); flowers 1–2 mm in diameter. Fruit a translucent white berry, flattened apically and discoid, ca. 6 mm long and 5 mm thick, flesh not viscid but the seed with thin viscid coating, endosperm dark green.

Branch parasites of evergreen montane forest formations known from only two collections in Costa Rica: *Kuijt* 2420 and 2468, both from near Villa Mills between 2,500 and 2,800 m elevation. The species is also known from Colombia and Ecuador at elevations over 2,500 m.

*Dendrophthora ambigua* is recognized by its thick rounded leaves, terete stems with paired scale leaves on lateral branches, and the very unusual spikes. Although these plants are very difficult to distinguish from species of *Phoradendron*, there are usually some spikes present with only two flower-series on opposing sides of the fertile internode. Also, there are spikes in which the two or three ranks above each bract are separated from those above the opposing bract by a somewhat flattened rachis. The impressions in the rachis made by fallen flowers and fruit are often continuous between the points of floral attachment to give a more or less continuous longitudinal groove.

***Dendrophthora costaricensis* Urban, Ber. Deutsch. Bot. Ges. 14:285. 1896.** *Phoradendron flavescens* Kuntze, Rev. Gen. 2:587. 1891, non Nuttall 1847. *P. crispum* Trel., Gen. Phorad. 77. 1916. *P. allenii* Trel., in Woodson & Schery, Ann. Missouri Bot. Gard. 27:307. 1940. *D. costaricensis* subsp. *poasensis* Kuijt, Wentia 6:51. 1961. Figure 9.

Small shrubs to 1 m tall, bisexual, leafy internodes 0.3–3.5 (6) cm long, 1–3 mm thick, glabrous and becoming wrinkled on drying, terete, lateral stems with 1 (2) pair of scale leaves 5–18 mm above the branching node, percurrent stems without paired scale leaves. Leaves well developed, petioles 1–6 mm long but not clearly distinguished from the laminae, 1–2 mm wide, the lateral margins continuous with the lamina margin; laminae 1.5–4.5 (6) cm long, 1–3 (4.5) cm broad, broadly obovate to elliptic-oblong or oblong (rarely suborbicular), abruptly rounded to bluntly obtuse at the apex, gradually narrowed to the attenuate base, margin entire and of somewhat thinner differentiated tissue (dry), venation palmate with the 3 major veins usually obscure on both surfaces. Inflorescences solitary in the axils of leaves (2 per node), 1–3 (4) cm long, the basal sterile internode 2–8

mm long with distal paired scale leaves fused at the base and flaring distally to become 2–3 mm broad, flowering internodes usually 2 (3, 4), the fertile internodes producing 10–30 flowers in basically 6 vertical (longitudinal) ranks but these often becoming obscured, male flowers 0.5–1 mm broad and distal on the internodes, as many as 12; female flowers forming later and proximal on the internodes but sometimes opening earlier, lacking staminodes. Fruit opaque white, globose to lobed, up to 6 mm in diameter, the calyx lobes persistent on the apex, seeds ca. 1.5 mm long and 1 mm thick, endosperm dark green.

Branch parasites of moist montane evergreen forest formations between (1,500) 1,800 and 3,300 m elevation; flowering throughout the year, but collected most often in the dry season: December to March. The species ranges from El Salvador to western Panama.

*Dendrophthora costaricensis* is recognized by its small opposite leaves rounded at the apex, terete stem with united scale leaves on branching stems, small spikes solitary in leaf axils, distinct basal flowerless internode, and crowded flowers in (more or less) six longitudinal ranks on each internode. The regularly spaced nodes and regular branching often produce a symmetrical treelike form. These plants are difficult to distinguish from species of *Phoradendron*.

***Dendrophthora squamigera*** (Benth.) Kuntze, Rev. Gen. 585. 1891. *Viscum squamigerum* Benth., Pl. Hartw. 190. 1845. *Phoradendron squamigerum* (Benth.) Oliver, Danske Vidensk. Meddel. 176. 1864. *Dendrophthora biserrula* Eichler, in Martius, Fl. Brasil. 5:104. 1868. *D. geniculata* Rizzini, Rodriguesia 18–19:219–220. 1956. Figure 9.

Small subshrubs (5) 10–40 cm tall, leafless and much branched with short crowded internodes, bisexual, the nodes demarked by paired scale leaves, internodes 2–50 mm long, 1–3 mm thick, glabrous and becoming roughly wrinkled when dry, terete. Leaves absent or 2 or 3 pairs of leaves at the base of the plant and grading into the scale leaves above, the scale leaves 1–2 mm long and opposite, partly united and with 2 sinuses or almost completely united and entire distally, 2–5 mm broad distally or becoming broader at branching nodes; the early-formed basal leaves up to 12 mm long, lanceolate and succulent, usually absent on flowering collections. Inflorescences solitary in the axils of scale leaves, 2 per node, 5–40 mm long, bisexual with the female flowers distal in an internode, male flowers formed later and proximal on the fertile internode, the spikes with a basal sterile internode (peduncle) 2–13 mm long and terminated by the cupulate united scale leaves, fertile internode usually 1 (2 or very rarely to 4), the 2 opposing spikes of a node often mirror images of each other, the fertile internode often somewhat flattened with the 2 longitudinal ranks of flowers imbedded in the narrow opposing edges (in a 2A arrangement), to as many as 40 flowers per internode and the flowering rachis to 4 mm broad, flowers ca. 1 mm broad. Fruit globose or somewhat oblate (compressed at base and apex), pearly to translucent white, 4–7 mm in diameter, drying yellowish, leaving shallow depressions in the rachis ca. 1 mm wide.

Branch parasites of higher montane forest formations between 2,400 and 3,500 m elevation; flowering throughout the year. The species ranges from the northern Andes of Colombia and Venezuela northward at higher elevations to Honduras and Guatemala.

*Dendrophthora squamigera* is recognized by the lack of foliage leaves, short internodes and symmetrical growth that often give a dense treelike form, flowers arranged in only two ranks, and the absence of terminal inflorescences. The restriction to higher altitudes and the usual yellowish green color of the plants further characterize this species. These plants are often dense and compact in their form, but it is not unusual to find individuals with longer thin internodes and a much more open habit. It is the most common parasite of the higher (above 3,000 m) subparamo formations that are dominated by ericaceous shrubs.

***Dendrophthora terminalis* Kuijt, Wentia 6:109–110. 1961. Figure 9.**

Small subshrubs ca. 20 cm high, leafless and with open regular branching, bisexual but female flowers rare, the nodes demarked by conspicuous paired scale leaves, internodes quite uniform in length, ca. 2 cm long and 1–2 mm thick (dry), glabrous and becoming wrinkled on drying, terete; prophylls prominent (2 mm long) and resembling the scale leaves, lateral and persistent on the base of branching stems. Leaves absent, the scale leaves 2–5 mm long, acute, opposing scale leaves united only near the base, the united basal margins concave and minutely erose, the paired scale leaves widely (4–6 mm) spread at branching nodes and when dry. Inflorescences terminal in those seen, made up of 3 or 4 fertile internodes, each fertile internode 5–10 mm long, the fertile rachis 1–1.5 mm thick, somewhat flattened with the 2 longitudinal ranks of flowers imbedded in the opposing narrow edges with the broader flat surface between the ranks, (2) 3–7 flowers per rank, flowers 1–1.5 mm broad, yellow.

This species is known only from a single collection by Alexander Skutch (3570) from Vara Blanca de Sarapiquí between Poas and Barba volcanoes at about 1,680 m elevation. The plant was collected in February and was found as a parasite on *Clusia*, which itself may have begun as an epiphyte.

*Dendrophthora terminalis* is very similar to *D. squamigera* and differs primarily in the terminal inflorescences, the prominent prophylls, and the larger, more acute scale leaves united only near the base. The regular branching and lack of foliage leaves are characteristic of both species. This species seems to have thinner and somewhat more openly branched stems than most specimens of *D. squamigera*, but some individual specimens of *D. squamigera* do have thinner stems branching more distantly. Lateral branches develop in the axils of scale leaves one or two internodes below the spikes, producing a somewhat dichasial habit.

**PHORADENDRON Nuttall**

Small- to medium-sized (3 m) shrubs, aerial (branch), parasites and attached to the host by specialized roots but with chlorophyll in the leaves and stems, bisexual or unisexual, glabrous in ours, young stems terete or angular, the nodes with a narrow constriction around the circumference (articulate), often breaking easily, sometimes thickened, the stems often bearing pairs of small (1–5 mm) basally united scale leaves just above the base of lateral branches and/or between the leaf-bearing nodes. Leaves opposite and decussate, articulate at the base, petioles often not clearly differentiated from the laminae, our species with well-developed coriaceous laminae, margins entire or slightly undulate, venation palmate to pinnate. Inflorescence axillary or rarely terminal, a thick spike with partly imbedded flowers, divided by opposing pairs of scale leaves into 1 basal sterile and 1 to several distal fertile internodes, the internodes with basal intercalary growth, the oldest flowers distal on the internodes and the youngest emerging from the proximal scale leaves (bracts), the flowers often in 4 longitudinal ranks with 2 alternate distal flowers (1A type), less often in 6 ranks per internode (1B type), and rarely in annular or in broad groups among our species, the spikes unisexual or bisexual; flowers very small and unisexual, perianth of 1 series of 3 (2–5) lobes, united near the base, valvate in bud, the male flowers with sessile or subsessile stamens at the base (opposite) the calyx lobes, anthers with 2 thecae; female flowers with inferior 1-locular ovary and 1 basal ovarian papilla, style short, stigma capitate. Fruit a fleshy, 1-seeded berry with viscid pulp, the endosperm copious and green; sepal lobes persistent.

A large American genus, mainly tropical, but extending into the temperate zones in the United States and in Argentina. The genus was reviewed in 1916 when 240 species were recognized and more than half described as new (see William Trelease, *The Genus Phoradendron, A Monographic Revision*, Urbana, Illinois).

The shrubby semiparasitic and epiphyte-like habit is often associated with thick semisucculent leaves, stems, and inflorescences. The articulate nodes, strictly



opposite leaves, glabrous parts (in ours), and flowers arising from depressions in the rachis further characterize the genus. The flowers in usually more than four vertical (longitudinal) ranks and lacking subtending bracteoles distinguish *Phoradendron* from similar plants found in most species of *Dendrophthora* and *Oryctanthus*. Some leafy species of *Dendrophthora* are very much like *Phoradendron*, but the difference in anthers seems to be a consistent distinction between the two genera.

The following account of *Phoradendron* species is probably the least adequate of any genus yet treated for the Flora Costaricensis series. At first it seemed that inadequacy of collection, the fragile and fragmentary nature of many specimens and unusual within-species variation were responsible for making species delimitation so difficult in *Phoradendron*. However, occasional collections suggest that hybridization between species may be another factor. The illustrations and keys are an attempt to characterize the commonly collected material. Neither keys nor illustrations are of much help when working with unusual collections that may represent variants, hybrids, or species not yet recognized in our flora. Nevertheless, we need more collections of these plants so that future workers can solve some of the problems posed by the material at hand.

- 1a Branching always dichotomous with the inflorescence solitary and terminal, pairs of small scale leaves present just above the branching node and midway between leaf-bearing nodes; rare plants of evergreen areas ..... *P. dichotomum*
- 1b Branching various, dichotomous or not, the inflorescences axillary to leaves. . . . 2a
- 2a Leaf-bearing nodes difficult to see because of the slightly expanded leaf bases, laminae lanceolate to falcate (curved), narrowed toward the base but widened and somewhat auriculate at the stem ..... *P. dipterum*
- 2b Leaf-bearing nodes not obscured by the leaf bases, petioles narrowed to the stem ..... 3a
- 3a All stems between leaf-bearing nodes with small (1–5 mm) pairs of scale leaves, these sometimes just above the node and obscure or not visible on older nodes, stems usually terete or only slightly 2- to 4-angled in early stages ..... 4a
- 3b Percurrent stems between leafy nodes lacking small pairs of scale leaves, scale leaves present on the lateral stems above branching nodes (note that branching nodes may occasionally appear to be percurrent when 1 branch fails to develop or is lost), stems sometimes flattened or angled in age ..... 9a
- 4a Paired scale leaves tubular or splitting, ca. 4 mm long, borne 2–8 mm above the branching node; laminae lanceolate to falcate and often acute apically; female spikes with the proximal (basal) half of the fertile internode lacking flowers; branching usually dichotomous; rare in collections ..... *P. acinacifolium*
- 4b Paired scale leaves short-tubular or a tube not apparent, borne 0–5 mm above the node; female spike with flowers throughout most of the length of the fertile internodes ..... 5a
- 5a Laminae usually somewhat rounded at the apex; branching often dichotomous; stems between leaf-bearing nodes almost always with only 1 pair of scale leaves ..... 6a
- 5b Laminae usually acute to acuminate at the apex; branching not usually dichotomous; stems between leaf-bearing nodes occasionally with 2 pairs of scale leaves ..... 7a
- 6a Laminae usually oblong, mostly rounded at the apex, often emarginate with a minute succulent tip, surface slightly rough in life, the plants often grayish or olive green; common in deciduous and semideciduous areas, 0–1,000 m elevation ..... *P. robustissimum*
- 6b Laminae usually narrowly ovate to lanceolate, often tapering gradually to the blunt apex and rarely emarginate, the surface smooth and lustrous in life, entire plant often with a reddish cast; common in eastern areas of the Central Highlands, evergreen areas from (0) 1,000–2,000 m elevation. . . . *P. obliquum*
- 7a Venation pinnate, the major veins flat and inconspicuous when the leaves are



dried, the laminae tapering gradually to base and apex, 1–4 (6) cm broad; 0–1,500 m elevation but most common in the evergreen lowlands

*P. piperoides*

- 7b Venation palmate, the major veins usually becoming raised and prominent when dry, the laminae often rounded at the base. . . . . 8a
- 8a Spikes usually borne in the axils of leaves; flowers in 6 longitudinal ranks on each internode; the fruit obscuring the rachis and nodes of the spike, pale orange-yellow; laminae 2–6 (8) cm broad; 600–2,000 m elevation . . . *P. flavens*
- 8b Spikes not usually borne in the axils of leaves, often in 2–4 groups along the stem between leaf-bearing nodes; flowers in 4 longitudinal ranks with 2 alternate distal flowers on each internode; fruit not usually obscuring the rachis, yellowish white; laminae (2) 4–10 cm broad; 0–1,000 (1,500) m elevation in evergreen formations . . . . . *P. crassifolium*
- 9a Laminae lanceolate to linear-lanceolate, to 15 (20) cm long but rarely more than 2.5 cm broad; plants of higher altitudes, (700) 1,000–3,000 m elevation . . . . . 10a
- 9b Laminae elliptic to narrowly ovate or narrowly oblong. . . . . 12a
- 10a Male flowers in 2 opposite disklike areas on each fertile internode, female flowers usually in an annular ring around the fertile internode (a whorl of usually 6 1-flowered ranks); leaves rarely curved and often drying dark; plants often found on *Quercus*, 1,500–3,000 m . . . . . *P. annulatum*
- 10b Male flowers never found in broad disklike groupings, female flowers with at least some ranks of 2 or more flowers, never a whorl of 1-flowered ranks . . . . . 11a
- 11a Laminae generally curved (falcate), to 20 cm long, but rarely more than 2 cm broad; male spikes with 6 ranks (of ca. 10 flowers each) per fertile internode; female spikes with usually 4 ranks (of 2 flowers) and 2 alternate distal flowers; most commonly found on the Pacific slope, (300) 1,000–2,000 m . . . *P. tonduzii*
- 11b Laminae only occasionally curved, never so long and narrow . . . . . 12a
- 12a Laminae usually elliptic to narrowly ovate or lanceolate, usually tapering to an acute apex, often more than 8 cm long . . . . . 13a
- 12b Laminae obovate, ovate, to narrowly oblong or very narrowly elliptic, usually rounded at the apex, rarely more than 7 cm long. . . . . 14a
- 13a Laminae with pinnate venation, lateral stems with 2 or 3 pairs of scale leaves between the branching node and the first leaf-bearing node; (900) 1,100–2,500 m . . . . . *P. undulatum*
- 13b Laminae with palmate venation, lateral stems with a single pair of scale leaves about halfway between the branching node and the first leaf-bearing node; 2,000–3,000 m . . . . . *P. sp. aff. undulatum*
- 14a Lateral stems with 2 pairs of scale leaves between the branching node and the first leaf-bearing node, young stems usually 2-angled or somewhat flattened; 1,000–2,000 m elevation in western Panama . . . . . *P. corynarthron*
- 14b Lateral stems with a single pair of scale leaves between the branching node and the first leaf-bearing node, young stems usually 4-angled in cross section; plants of lowland (0–1,000 m) deciduous and evergreen formations. (Note that specimens with rounded stems from above 1,400 m elevation keying to this dichotomy are probably plants of the genus *Dendrophthora*). . . . . 15a
- 15a Laminae usually narrowly oblong or elliptical, bluntly rounded at the apex; fruit with a smooth or wrinkled surface; common in Costa Rica . . . . . *P. quadrangulare*
- 15b Laminae usually broadly obovate, with an apical notch or bilobed at the apex (rarely rounded); surface of the fruit with small tubercles or projections; rarely collected in Central America . . . . . *P. mucronatum*

**Phoradendron acinacifolium** Eichler, in Martius, Fl. Brasil. 5, pt. 2:117. 1868. *P. robaloense* Woodson ex Rizzini, Ann. Missouri Bot. Gard. 47:282. 1962. Figure 11.

Shrubs, 1–2.5 m tall, basal stems up to 7 cm in diameter, apparently unisexual, leafy internodes 2–10 cm long, 2–6 mm thick, terete, stems usually branching dichotomously and percurrent stems absent, 1st lateral internodes with united pairs of scale leaves forming a tube ca. 4 mm long a little (2–8 mm) above the branching node. Leaves usually

asymmetric and slightly curved, petioles 4–15 mm long, lateral ridges continuous with the lamina margins; laminae 4–20 cm long, 1.4–5 cm broad, lanceolate to falcate or narrowly ovate, tapering gradually to the usually acute (rarely blunt and rounded) apex, sometimes with a minute succulent tip, tapering to the attenuate and often unequal base, margin entire but undulate on drying, venation palmate with 5–7 primary veins, the major veins often obscure. Inflorescences usually 2 (3) per leaf axil, 4–6 per node, the sterile rachis (peduncle) usually drying very (1–2 mm) thin; male spikes to 8 cm long, with 3 or 4 fertile internodes, each to ca. 2 cm long, male flowers present throughout the length of the internode or absent near the base, in 4 longitudinal ranks of 6–10 flowers each; female spikes 3–5 cm long, rachis with 3 or 4 fertile internodes bearing flowers only in the distal half, each fertile internode 2–15 mm long, female flowers in 4–6 longitudinal ranks of only 1–3 flowers each. Fruit a large ovate berry with acute apex ca. 8 mm long and 6 mm thick but much smaller (5 × 2 mm) and narrowly ovoid or subcylindrical when dry.

Branch parasites of evergreen montane forests between 700 and 2,000 m elevation in Costa Rica; flowering and fruiting collections have been made between January and August. The species apparently ranges southward to Paraguay.

*Phoradendron acinacifolium* is recognized by the usually dichotomous branching, slightly curved somewhat falcate leaves, and slender spikes with the fertile internodes (of the female) bearing flowers only in the distal part. Description of the male flowers and inflorescences is based on only two collections: *Stone 3121* from above Tapanti, Cartago, and *Stern et al. 1992* from near Boquete, Chiriqui, Panama.

***Phoradendron angustifolium*** (H.B.K.) Nuttall, J. Acad. Nat. Sci. Philadelphia, ser. 2, 1:185. 1847. *Loranthus angustifolius* H.B.K., Nov. Gen. Sp. Pl. 3:442. 1820. *Viscum angustifolium* (H.B.K.) DC., Prodr. 4:281. 1830. *V. ensifolium* Pohl, in DC., loc. cit. *Phoradendron ensifolium* (Pohl) Nuttall, loc. cit.

In the paper on mistletoes of Panama, *P. corynarthron* and *P. tonduzii* are placed in synonymy under *P. angustifolium* (Kuijt, Ann. Missouri Bot. Gard. 65:744, 1978). In the present treatment, both *P. corynarthron* and *P. tonduzii* are retained, because they are usually easy to recognize and distinguish in Costa Rica, and because they do not conform very well with the type description of *P. angustifolium* or with a majority of the South American material associated with that name. If the broader concept of *P. angustifolium* proves sound, then the rank of subspecies might be considered as appropriate for the two groups of specimens here placed under *P. corynarthron* and *P. tonduzii*.

***Phoradendron annulatum*** Oliver, Vidensk Meddel. Dansk Naturhist. Foren. Kjoebenhavn 1864:176. 1865. Figure 10.

Large shrubs 1–2 m tall, probably unisexual, leafy internodes 2–8 cm long, 2–9 mm thick, slightly flattened at first but soon terete, drying dark, percurrent stems without paired scale leaves, lateral stems with distinct paired scale leaves 5–15 mm above the branching node. Leaves symmetrical or somewhat curved and asymmetrical, petioles 5–15 mm long but gradually merging with the lamina and the lateral ridges continuous with the lamina margins; laminae 8–15 cm long, 1–2.5 cm broad, linear-lanceolate to somewhat falcate, tapering very gradually to the acute or blunt apex, tapering gradually to the attenuate base, margin entire, laminae drying stiffly coriaceous and the margins occasionally slightly undulate, venation palmate to subpalmate with 3 major veins, venation obscure. Inflorescences solitary in the leaf axils (2 per node), very short (1–3 cm) and thick, drying dark; male spikes with 4 or 5 very short (4–6 mm) fertile internodes, each fertile internode with 2 opposite groups of 10–15 densely crowded flowers, the flowers forming a well-defined cushion-like area circular to ovate in outline and without floral ranks or seriation; female spikes 1–3 cm long, usually of 4 rounded internodes 3–5 mm long and

each bearing only a single whorl (annulus) of 6 flowers deeply imbedded in the rachis (6 longitudinal ranks of 1 flower each from a modified 1A arrangement). Fruit not seen, fruiting spikes ca. 3.5 cm long.

Branch parasites of higher montane evergreen forest formations between 1,500 and 3,000 m elevation; fertile collections have been made in July, August, and December. The species, as presently understood, is endemic to the Cordillera de Talamanca in Costa Rica and the adjacent highlands of western Panama.

*Phoradendron annulatum* is distinguished by its thick linear-lanceolate leaves on thick rounded stems, the scale leaves about 1 cm above the base of lateral branches, lack of scale leaves on percurrent nodes, the unusual arrangement of male flowers in opposite circular areas, and the equally unusual "annulus" of flowers on the female spikes. These plants often have long unbranched distal stems with short thick internodes (as in Davidson 1996 and Evans et al. 2002). This species is very closely related to *P. conzattii* Trel. of Mexico, but that species has longer, more falcate leaves and the female flowers more numerous in each fertile internode. Material ascribed to this species in the Flora of Guatemala was apparently misidentified (Fieldiana, Bot. 24, pt. 4:69. 1946), as neither *P. annulatum* nor *P. conzattii* have been collected from the area between Mexico and Costa Rica.

***Phoradendron corynarthron*** Eichler, in Martius, Fl. Bras. 5, pt. 2:115. 1868, e descr. *P. davidsoniae* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22:17. 1940. Figure 9.

Small shrubs of yellowish brown appearance, leafy internodes 1–5 cm long, 1–3 mm thick, somewhat flattened or 2-ridged in early stages but soon becoming terete, scale leaves absent on percurrent stems, the 1st lateral internodes with 2 pairs of scale leaves, the lowest ca. 1 cm above the base of the lateral branch and the 2nd usually 1–2 cm above the 1st. Leaves usually symmetrical and straight (rarely curved), petioles ill defined, 1–5 mm long, the lateral winglike margins continuous with the lamina margins; laminae 4–8 cm long, 8–14 mm broad, lanceolate to very narrowly elliptic-oblong, gradually or abruptly narrowed at the usually blunt apex, very gradually narrowed at the cuneate to attenuate base, margin entire and drying as a rim of thinner slightly differentiated tissue, laminae drying very stiffly chartaceous or subcoriaceous but thin, venation palmate, the 3 central primary veins reaching the distal half of the lamina but obscure beneath. Inflorescences solitary in the axils of leaves, 2 per node, 1–3 cm long or becoming 4 cm long in fruit, flowering internodes with a basal sterile rachis 2–8 mm long and ca. 1 mm thick (dry); male spikes not seen; female spikes with 2–4 fertile internodes, female flowers in 6 vertical ranks of usually 1 or 2 flowers each (ca. 8–14 flowers per internode). Fruit becoming globose and white, 3–5 mm in diameter.

Branch parasites of premontane and lower montane wet forest formations between 1,000 and 2,200 m elevation in western Panama; collected with flower or fruit between March and July. The species is known only from around Volcan Baru (Chiriqui) and the Boquete district in the province of Chiriqui, Panama.

*Phoradendron corynarthron* is recognized by the smaller very narrow symmetrical leaves, the consistent presence of two pairs of scale leaves on the lateral stems above the branching node, solitary spikes in the leaf axils, few-flowered internodes with a basal sterile rachis often equaling in length the fertile portion, and the restricted mid-elevation habitat. While not known in Costa Rica, it may be expected in the eastern part of the Talamanca range. This species is related to *P. tonduzii*; see the discussion under that species and under *P. quadrangulare*. Recently, *P. corynarthron* has been placed into synonymy under *P. angustifolium*; see the discussion under that species.

**Phoradendron crassifolium** (Pohl ex DC.) Eichler, Fl. Brasil. 5, pt. 2:125. 1868. *Viscum crassifolium* Pohl ex DC., Prodr. 4:280. 1830. *P. crassifolium* var. *pittieri* Trel., Gen. Phorad. 145, pl. 215. 1916. Figure 11.

Shrubs, apparently bisexual, stems usually percurrent, leafy internodes 3–15 cm long, (1.5) 2–6 mm thick, terete, percurrent stems with a small pair of scale leaves above the leafy node, usually with 2–4 pairs of deciduous scale leaves evenly spaced between the leafy nodes. Leaves opposite, articulate at the stem, petioles ca. 5 mm long, difficult to distinguish because of the attenuate lamina base, margins of the lamina continuous with the lateral ridges of the petiole; laminae 6–16 cm long, (2) 4–10 cm broad, ovate to elliptic-ovate, elliptic-oblong, or oblanceolate, tapering gradually to the acute to acuminate apex, tapering gradually or abruptly to the cuneate or attenuate base (sometimes rounded basally in the broader lamina), margin entire but often undulate on drying, the laminae drying stiffly coriaceous, venation subpalmate with the 5 major veins free or united for 1–2 cm above the base, major veins obscure in fresh material but often raised on both surfaces and readily visible when dried. Inflorescences usually in the axils of small scale leaves and occasionally in the axils of larger leaves, 1 or 2 (rarely 3) per axil (2, 4, or rarely 6 per node), spikes 1–3 cm long, usually with 4–7 small closely spaced fertile internodes, flowerless rachis ca. 1.5 mm thick (dry), paired fertile scale leaves ca. 1.5 mm long and 2 mm broad (apex to apex), flowers in 4 vertical ranks of only 1 or 2 (3) flowers each, distal flowers in the internode may be staminate. Fruit 2–3 mm long, ca. 2.5 mm thick (dry), pale orange-yellow when ripe, somewhat ellipsoid, 4–8 fruit per internode, fallen fruit leaving a depression 1–2 mm broad with a minutely erose margin.

Branch parasites of wet evergreen forest formations and known in Costa Rica only from the southern half of the Pacific slope (western area of the General Valley to Golfo Dulce) from 30 to 800 m elevation, but to 1,500 m in adjacent Panama; apparently flowering throughout the year. The species ranges from Guatemala southward to Peru and Brazil.

*Phoradendron crassifolium* is recognized by the thick leaves, with subpalmate venation usually tapering at both apex and base, and the short spikes usually borne in the axils of two to four pairs of small scale leaves on the leafless stems between pairs of foliage leaves. The species is poorly represented in collections, and it may be more widely distributed in Costa Rica than present collections indicate. This is the only Central American *Phoradendron* in which the inflorescences arise from the axils of scale leaves (intercalary cataphylls) as well as from the axils of leaves or fallen leaves (but not all flowering stems exhibit this peculiarity).

**Phoradendron dichotomum** (Bert.) Krug & Urban, Bot. Jahrb. 24:48. 1897. *Viscum dichotomum* Bertero, in Sprengler, Syst. 1:488. 1824, non D. Don, Prod. Fl. Nepal. 147. 1825. Figure 10.

Shrubs, bisexual, with slender dichotomizing growth, leafy internodes 3–12 cm long, 1.5–4.5 mm thick, round or slightly angular in early stages, branching dichotomous because of terminal inflorescences (percurrent stems absent), a pair of scale leaves present about midway between the leaf-bearing nodes and a pair of scale leaves also present just above the leaf-bearing node. Leaves symmetrical or slightly asymmetric, petioles 2–8 mm long but gradually merging with the lamina base; laminae 5–12 cm long, 1.7–4 cm broad, lanceolate to narrowly ovate, gradually tapering to the acute apex, acute to attenuate at the base, margin entire and usually drying undulate, the laminae drying coriaceous but relatively thin, venation palmate or subpalmate with usually 5 primary veins, the major veins usually obscure. Inflorescences 1 and terminal or occasionally with 2 additional lateral spikes on 1 side of the dichotomizing twigs, the spikes 3–6 cm long, with up to 6 (7) fertile internodes, a sterile basal internode often present, the fertile internodes to 16 mm long and apparently bisexual with the male flowers distal, the flowers in 6 longitudinal



ranks or 4 ranks with 2 alternate distal flowers (1B or less often 1A), flowers borne in deep depressions with entire margins. Fruit and undeveloped flowers often present in the same areas of the fertile internodes, fruit globose and ca. 3 mm in diameter (dry).

Apparently rare branch parasites of evergreen forest formations and known in Central America from only two collections: *Tonduz 13142*, near Tucurrique, Cartago, at 635 m altitude, and *Williams et al. 29155*, from near Sta. Maria de Ostuma, Cordillera Central de Nicaragua, at 1,400 m altitude. These collections were made in January and February. The species ranges to northern South America and the West Indies.

*Phoradendron dichotomum* is the only species of the genus in our area with truly terminal spikes; however, these may fall off, and paired lateral spikes may be found at some nodes. In any event, virtually all the stems exhibit dichotomous branching. Scale leaves present in the middle of stems between leaf-bearing nodes as well as at the base of all stems and the bisexual(?) fertile internodes of the spikes further distinguish this species.

**Phoradendron dipterum** Eichler, in Martius, Fl. Brasil. 5, pt. 2:109–110. 1868. Figure 10.

Shrubs, bright green to olive green, bisexual, leafy internodes 2–9 cm long, 2–6 mm thick, somewhat flattened or 4-angled in cross section (in ours) or prominently 2- to 4-winged, becoming terete, percurrent stems without paired scale leaves, 1st lateral internodes with a pair of scale leaves at the base just above the branching node. Leaves symmetrical or asymmetrical, sessile and the petiole absent; laminae 5–13 cm long, 1.5–3 (4) cm broad, narrowly lanceolate or falcate to ovate-lanceolate, or narrowly oblong, tapering gradually or abruptly to the rounded apex, tapering gradually to the obtuse or rounded and clasping base, margin at the base usually revolute downward and almost auriculate, 5–10 mm broad across the base, the lamina edge orange in life, entire or undulate dried, venation palmate with 3–5 primary veins slightly raised on the upper surface (dry). Inflorescences 1 or 2 in the axils of leaves (2–4 per node), unisexual, male and female at different but sometimes adjacent nodes, flowers often irregularly arranged in the fertile internodes; male inflorescences to 8 cm long with 4–7 fertile internodes, each fertile internode ca. 1 cm long, the flowers usually in 6 longitudinal ranks of 6 or 7 flowers each, united pairs of scale leaves (fertile bracts) ca. 2 mm long and 3–4 mm broad apically; female inflorescences to 5 cm long with 3–5 fertile internodes, the female flowers usually in 6 longitudinal ranks of ca. (2–) 5 flowers each. Fruit an orange-tipped white spherical berry ca. 2 mm in diameter, flesh transparent.

Apparently rare branch parasites of partly deciduous and evergreen forest formations between about 1,000 and 2,000 m elevation in Central America. The species is known in Costa Rica only from a single collection (*Kuijt 2587*) from El Alto, Cartago, and flowering in August. The species, as interpreted by *Kuijt (1964)*, ranges from southern Mexico to northern Argentina.

*Phoradendron dipterum* is recognized by its narrow leaves clasping the stems at their base with recurved auriculate-like margins, the palmate venation, the long internodes with ridges or wings in early stages, the male and female spikes sometimes found at adjacent nodes, and the fertile internodes with usually more than 25 flowers. The species is known from only a few collections in Central America. Material from Oaxaca, Mexico, under the name *P. auriculatum* Trelease has the stems prominently winged and quadrangular, and the leaves are shorter and more ovate-oblong. With so few samples at hand, it is not possible to decide at this time the proper status of these northern elements. In most of these collections, the flowers are deeply imbedded in the rachis, and the edges of the floral depressions are minutely erose.

**Phoradendron flavens** (Sw.) Grisebach, Fl. Brit. W. Ind. 313. 1864. *Viscum flavens* Swartz, Prodr. Veg. Ind. 32. 1788. *P. quinquenervium* Krause, Notizbl. Königl. Bot. Gart. Berlin 5:264. 1912. *P. supravenulosum* Trel., Gen. Phor. 154. 1916. Figure 11.

Shrubs 1–2 m broad, branch parasites, apparently unisexual, leafy internodes 2–7 cm long, 1.3–4 (6) mm thick, terete or somewhat 2- or 4-angled in early stages, percurrent stems with a pair of keeled scale leaves ca. 1 cm above the basal node, the 1st lateral leafy internode with a pair of scale leaves near the base and a 2nd pair at ca.  $\frac{1}{3}$  the length to the next leafy node. Leaves opposite, somewhat articulate at the stem, petioles 1–6 mm long, not clearly distinguished and with lateral ridges continuous with the lamina margins; laminae 4–11 (14) cm long, 2–6 (8) cm broad, ovate to elliptic-ovate or elliptic, occasionally lanceolate or asymmetric and curved, tapering gradually or abruptly to the acute to acuminate apex (occasionally obtuse), tapering gradually or abruptly to the attenuate base, margin entire, drying stiffly chartaceous to subcoriaceous, venation palmate or subpalmate with 3 or 5 primary veins, the 3 central primaries reaching the distal part of the lamina, the major veins often raised on the surface of the dried leaves, secondaries obscure. Inflorescences at first solitary but often with 1 or 2 additional developing in leaf axils (2–6 per node), the spikes 2–6 cm long, secondary spikes subtended by sterile scale leaves, the paired fertile scale leaves ca. 3 mm broad (tip to tip) and 2–3 mm long and keeled, sterile portions of the rachis ca. 0.8–2 mm thick (dry), with 6 vertical ranks of 2–7 flowers each, male spikes with usually 6–15 flowers per internode, the female with 30–50 flowers. Fruit becoming contiguous and obscuring the rachis, 2–3 mm in diameter, globose, yellowish white, pulp viscid and transparent, fertile internodes to 15 mm long.

Branch parasites of wet evergreen and moist mountain forest formations between 600 and 1,900 m elevation on both the Caribbean and Pacific slopes of Costa Rica; probably flowering throughout the year, but not collected in July–August or October and December. The species ranges from Guatemala and Belize to northern South America and the southern Caribbean Islands.

*Phoradendron flavens* is recognized by the scale leaves present on the often slender percurrent stems, leafy nodes often with two older and four younger spikes, laminae often narrowed to both apex and base with the palmate venation readily apparent when dry, and the flowers usually in six vertical ranks. This species is closely related to *P. piperoides*, but is easy to separate by the obviously palmate venation of the usually broader leaves. Typical material of this species is distinguished by the ovate to oblong leaves with three primary veins distinctly raised above when dried and the succulent fruits becoming contiguous so that the nodes are not visible on the spike.

*Phoradendron woodsonii* Trelease, discussed by Kuijt (1974) in his recent review of the Panamanian species, would key out here if found in the Costa Rican flora. This species has two to four pairs of scale leaves on its internodes, and it differs from *P. flavens* in other ways. *Phoradendron flavens*, *P. crassifolium*, *P. piperoides*, and *P. woodsonii* appear to form a closely related group, and it is possible that hybridization occurs among them.

**Phoradendron mucronatum** (DC.) Krug & Urban, Bot. Jahrb. 24:34. 1897. *Viscum mucronatum* DC., Prodr. 4:282. 1830.

Small shrubs, leafy internodes to ca. 3 cm long and 3 mm thick, usually with 4 prominent longitudinal ridges and square in cross section, glabrous, percurrent stems without scale leaves but often with an articulation just above the node, lateral stems with a pair of scale leaves ca. 3 mm long just above the node. Leaves short and broadly rounded, petioles 1–3 mm long; laminae 1–4 cm long, 1–3 cm broad, broadly obovate to suborbicular, abruptly rounded distally and emarginate to bilobed at the apex, abruptly narrowed at the base, margins entire, laminae drying yellowish green and subcoriaceous, venation palmate

with the 3 or 5 primary veins often visible on the upper surface. Inflorescence 0.5–3 cm long, usually solitary in the axils of leaves or fallen leaves, each fertile internode 2–5 mm long, usually with only 1 flower in each of 4 ranks resulting in a whorl of 4 flowers (rarely 6) per internode. Fruit ca. 2.5 mm in diameter, with persisting and erect perianth lobes ca. 0.5 mm high, surface covered with small papillae that give a muricate or tuberculate appearance.

A species of evergreen or partly deciduous lowlands often found near mangroves, lakes, and rivers in Central America; from sea level to 800 m elevation. Rarely collected in Mesoamerica, but ranging from the Yucatan peninsula and the West Indies to southern Brazil.

*Phoradendron mucronatum* is a very distinctive member of the genus with small rounded leaves deeply emarginate or bilobed at the apex, short four-ridged internodes, short spikes often with only one whorl of flowers per fertile internode and unusual surface of the fruit. Although known from Panama and Guatemala, this species has not been collected from Costa Rica; it is likely to occur in the Caribbean lowlands.

***Phoradendron obliquum* (Presl) Eichler, Fl. Brasil. 5, pt. 2:134. 1868. Figure 11.**

Large shrubs to 2 m in diameter, often pendent, unisexual, the branches often forking dichotomously, leafy internodes 2–15 cm long, 2–8 mm thick, young stems slightly flattened or round and the older terete, percurrent stems rare and with paired scale leaves just above the node, lateral stems with paired scale leaves just above the branching node and somewhat tubular distally (a second pair of scale leaves rarely present ca. 1 cm above the node). Leaves often asymmetric and somewhat curved, petioles to 15 mm long but difficult to distinguish from the laminae, the winged margins continuous with the lamina margins; laminae 6–15 (23) cm long, 2–7 (9) cm broad, narrowly ovate to lanceolate and sometimes slightly curved, tapering gradually to the acute or bluntly rounded apex, rounded or gradually to abruptly narrowed at the attenuate base, margin entire but drying undulate, the laminae drying stiffly coriaceous, venation palmate, subpalmate, or pinnate with the secondaries arising in the lower 4th of the midvein, the major veins usually 5 and only the central 3 subparallel, often obscure (dry). Inflorescences 3–5 cm long, the male as many as 12 per node, the female 2–6; male spikes unknown (see discussion); female spikes with 3 or 4 fertile internodes with 4 longitudinal ranks of 2–4 flowers each and 2 distal alternating flowers. Fruit ellipsoid to somewhat cylindrical, ca. 3–5 mm long and 2–3 mm thick (dry), depressions in the rachis to 3 mm in diameter and with an entire edge.

Branch parasites of evergreen and partly deciduous forest formations between sea level and 1,400 m elevation; probably flowering throughout the year. This species ranges from Costa Rica to Peru; our material has been collected in the Central Highlands and their slopes and southwestern Costa Rica.

*Phoradendron obliquum* is recognized by the frequent dichotomous branching, scale leaves usually present just above the node on all stems, thick larger leaves usually tapering to a narrowed apex and often slightly curved, and flowers throughout the length of the fertile internodes. In life, the plants are often characterized by a reddish color and leaves with a shiny-glossy surface. The latter character differentiates this species from the closely related *P. robustissimum* which has rough-surfaced leaves in life. Unfortunately, this character disappears on drying, and some specimens may be very difficult to place in one or the other species. The two species are very closely related, and intermediate plants or populations may exist: see the discussion under *P. robustissimum*.

A survey (Kuijt, 1964) of almost 30 plants near the continental divide between Tres Rios and Cartago disclosed no staminate plants or spikes. A more intense study of plants on the University campus near San Pedro found that male flowers are extremely rare (1% to 2%), occurring as the lowest (proximal and last devel-

oping) flowers of a floral rank in occasional fertile internodes. The fact that these populations were producing fruit suggests that these plants may have been reproducing asexually (Kuijt, 1964).

This species has been the subject of a thesis by R. E. Zurcher: Las Lorantheaceae que parasitan el laurel, *Cordia alliodora*, en Costa Rica y sus posibilidad de control con inyecciones de hierbicidas al tronco del huesped, Inst. Interamer. Ciencias Agric., Turrialba, 1958.

**Phoradendron piperoides** (H.B.K.) Trelease, Genus Phoradendron 145. 1916. *Loranthus piperoides* H.B.K., Nov. Gen. & Sp. 3:443. 1820. *P. biolleyi* Krause, Notizbl. Königl. Bot. Gart. Berlin 5:264. 1912. Figure 11.

Small shrubs, epiphyte-like hemiparasites, bisexual, the stems often trailing, leafy internodes 2–8 (10) cm long, 1.5–4 mm thick, terete, percurrent stems with a pair of reduced opposite scale leaves just above the node and often difficult to see, the first lateral internode with 1–5 pairs of scale leaves, 1 pair often near the center of the 1st lateral internode. Leaves opposite, petioles 1–4 (7) mm long, 1–2 mm broad, margins of the lamina continuous with the wings of the petiole; laminae 3–11 (14) cm long, 1–4.5 (6) cm broad, elliptic to oblong or narrowly obovate, acuminate to acute at the apex, usually tapering to the acute or attenuate base, margin entire but undulate on drying, the laminae drying coriaceous, glabrous and smooth, venation pinnate with 2–3 pairs of major secondary veins but these usually obscure. Inflorescences 1–3 per leaf axil (2–6 per node), very rarely terminal, the spikes 3–8 cm long with 1–3 sterile internodes near the base, the paired fertile scale leaves ca. 2.3 mm broad (apex to apex), sterile portion of the spike ca. 1 mm thick (dry), fertile internodes 6–11, usually with 4 longitudinal ranks of 2–4 flowers and 2 alternate distal flowers, rarely to 28 flowers per internode. Fruit spherical to ellipsoid, ca. 3 mm in diameter and yellowish to orange when ripe, separate from each other when dried.

Branch parasites of evergreen and partly deciduous forest formations between sea level and about 1,500 m elevation on both the Caribbean and Pacific sides of Costa Rica; apparently flowering throughout the year, but not collected in October and November and with the majority of collections made in February and August. The species ranges widely over the American tropics.

*Phoradendron piperoides* is recognized by the small paired scale leaves on all the slender and usually terete stems, medium-sized laminae tapering to both apex and base with usually obscure pinnate venation, and the inflorescences usually in axillary clusters at leafy nodes. The scale leaves just above the nodes of percurrent stems are often difficult to see or are represented only by opposite scars. This is one of Costa Rica's most abundant species of *Phoradendron*, especially common in the wet lowlands. It is particularly abundant in the Limon region on cacao and shade trees.

**Phoradendron quadrangulare** (H.B.K.) Krug & Urban, Bot. Jahrb. 24:35. 1898. *Loranthus quadrangularis* H.B.K., Nov. Gen. & Sp. 3:444. 1818. *P. ceibanum* Trel., Genus Phoradendron 110. 1916. *P. rensonii* Trel., loc. cit. 105. *P. venezuelense* Trel., loc. cit. 111. *P. corynanthron* var. *seibertii* Trel., Ann. Missouri Bot. Gard. 24:187. 1937. *P. paquitatum* Trel., Publ. Field Mus. Nat. Hist., Bot. Ser. 18:405. 1937. *P. herrerenense* Trel., Ann. Missouri Bot. Gard. 27:307. 1940. *P. sonanum* Trel., loc. cit. 308. *P. seibertii* (Trel.) Rizzini, loc. cit. 47:285. 1960. Figure 9.

Small shrubs, bisexual(?), branches usually erect and often branching dichotomously, leafy internodes, 1–8 cm long, 1–4 (6) mm thick, with 4 distinct longitudinal ridges but becoming rounded in age, often slightly thickened beneath the node, percurrent stems lacking fused pairs of scale leaves, 1st lateral stems with a pair of fused scale leaves just



above the branching node. Leaves usually symmetrical and straight, subsessile or with poorly defined petioles 0–4 (6) mm long, with lateral ridges continuous with the lamina margins; laminae 2.5–6 (7.5) cm long, 1–2.3 cm broad, very narrowly oblong, to narrowly elliptic or very narrowly obovate, rounded to bluntly obtuse at the apex, cuneate to attenuate at the base, margin entire, the laminae drying very stiffly chartaceous to subcoriaceous and often becoming grayish green, venation palmate with 3 or 5 primary veins, the 3 central veins reaching the distal part of the leaf, the major veins slightly raised or obscure (dry). Inflorescences 1 or less often 3 in each leaf axil (2–6 per node), spikes 1.5–3 (5) cm long, peduncle 2–6 mm long, flowering axis with 4–6 fertile internodes, the fertile pairs of scale leaves often small and inconspicuous, male and female spikes quite similar, the flowers in 4 vertical ranks of 2–4 flowers (very rarely to 7 in male spikes), and 2 alternating distal flowers, usually up to 18 flowers per fertile internode. Fruit globose, to 4 mm in diameter, yellow to yellow-orange.

Branch parasites most often found in evergreen and partly deciduous (tropical moist and premontane moist) forest formations below 1,000 m in elevation; flowering throughout the year. The species ranges from southern Mexico to northern South America and the West Indies.

*Phoradendron quadrangulare* is characterized by the small- to medium-sized leaves that are very narrow and abruptly rounded at the tip, the four-angled young stems, short slender spikes with few fertile internodes (or the internodes difficult to distinguish because of the very small paired scale leaves), and the apparent preference for semideciduous lowland habitats. The present circumscription of this species includes considerable variation in inflorescence morphology, but the laminae are rather uniform. For example, one of the very few collections from the wet Caribbean lowlands (*Lent* 1926 from Tirimbina, Sarapiquí, Heredia) has very narrow stems, distinctly petiolate leaves, and short spikes with very few (three to five) flowers per fertile internode. Material from Venezuela often has short-cylindrical or ellipsoid fruit, whereas ours appears to be uniformly globose as interpreted from the dry collections.

Several collections from near Tilaran (*Standley & Valerio* 44983 and 45577, *Williams, Molina, & Williams* 26606) key to this species, but are perhaps more closely related to *P. corynarthron* and *P. tonduzii*. The leaves of these specimens are a bit larger, but of much the same shape, as *P. quadrangulare* and *P. corynarthron*. However, they lack the angled stems of *P. quadrangulare* and the second set of scale leaves (on lateral stems) of *P. corynarthron*. These collections also lack the falcate leaves and two-ridged stems of *P. tonduzii*. All three species and the Tilaran material have very similar inflorescences and appear to be closely related. Perhaps the collections from Tilaran represent an unusual population of mixed parentage. The type of *P. dodgei* (*Dodge* 6200) from the same area, while having many of the characteristics of *P. tonduzii*, does resemble the specimens referred to above and may be intermediate between them and typical *P. tonduzii*. All these collections come from altitudes beneath those at which *P. corynarthron* and *P. tonduzii* are usually found.

***Phoradendron robustissimum*** Eichler, in Martius, Fl. Brasil. 5, pt. 2:122. 1868. *P. falcifolium* Trel., Gen. Phorad. 79. 1916. *P. pergranulatum* Trel., Ann. Missouri Bot. Gard. 27:308. 1940. Figure 11.

Shrubs to 1 m or more, dark green or grayish green, unisexual, usually branching dichotomously, leafy internodes 2–10 cm long, 2–6 mm thick, usually terete, percurrent stems infrequent, both percurrent and lateral stems with a single (rarely 2 or 3) pair of united scale leaves ca. 5 mm above the node, 2 spikes often peripheral to the aborted apex with vegetative laterals developing axillary to prophylls of the spikes or vice versa. Leaves

symmetric or the larger often asymmetric, petioles 2–15 mm long but not easily distinguished from the attenuate leaf base, broader than thick and with the lateral margin continuous with the lamina margin; laminae 3.5–10 (14) cm long, 2–5 (8.5) cm broad, oblong to ovate-oblong or somewhat spatulate, abruptly rounded at the apex, often emarginate with a minute succulent tip, abruptly narrowed at the attenuate base, margin entire with a thin brownish edge, the laminae drying stiffly coriaceous, surfaces with a slightly rough texture in life and, when dry, venation palmate to pinnate with the secondaries arising from the lower 3rd of the midvein, usually subpalmate, with usually 5 major veins and these often obscure. Inflorescences dimorphic, the male much thinner than the female, 1 to several per leaf axil or the males as many as 12 on older nodes; male spikes to 11 cm long, with 4–6 fertile internodes 1–2 cm long, sterile rachis ca. 1–2 mm thick, male flowers in 4 (6) longitudinal ranks of ca. 10 flowers each and with 2 alternating terminal flowers (1A arrangement) female spikes to ca. 6 cm long with 3–5 fertile internodes, the central (longer) internodes 1–2 cm long with 4 ranks of 4 or 5 flowers each and 2 alternate terminal flowers (1A arrangement). Fruit elliptic-ovate or cylindric (dry) and about 4 mm long and 2 mm thick, yellowish to dusty yellow-green.

Branch parasites of both evergreen and deciduous lowland forest formations below about 1,000 m in Costa Rica; apparently flowering throughout the year. The species ranges from southern Mexico to Venezuela.

*Phoradendron robustissimum* is recognized by the stiff oblong leaves usually with bluntly rounded apices, frequent dichotomous forking of the stems, slender male spikes often more than eight at older nodes, and usual restriction to lower (0 to 500 m) altitudes on the Pacific slope. This species is related to *P. obliquum* and may be difficult at times to separate from specimens of that species; see discussion under *P. obliquum*.

***Phoradendron tonduzii*** Trelease, Gen. Phorad. 67. 1916. *P. cooperi* Trel., loc. cit. *P. dodgei* Trel., Publ. Field Mus. Nat. Hist., Bot. Ser., 18:405. 1937. *P. novae-helvetiae* Trel., Ann. Missouri Bot. Gard. 27:307. 1940. Figure 10.

Shrubs, often orange-brown or yellow-brown, to ca. 1 m broad and often pendulous, unisexual, leafy internodes 1–10 cm long, 1–5 mm broad, with 2 opposing ridges and somewhat flattened in early stages, scale leaves absent on percurrent stems, the 1st lateral internode with 1 or rarely 2 pairs of scale leaves near the base. Leaves opposite, articulate at the stem, usually asymmetric, petioles 5–20 mm long but not really distinguishable from the lamina base; laminae 6–15 (20) cm long, 0.5–2 (3) cm broad, very narrow and usually curved (falcate) to narrowly lanceolate, tapering gradually to the acuminate apex, tapering gradually to the attenuate base, margin entire or undulate, laminae drying very stiffly chartaceous, smooth and glabrous, venation palmate with 3–6 primary veins the 3 central primaries subparallel and reaching the distal half of the lamina, slightly raised and usually visible (dry). Inflorescences 1–3 in the axils of leaves (2–6 per node), spikes 3–7 cm long, usually without basal sterile scale leaves; the male spikes with ca. 4–8 fertile internodes, flowerless rachis 0.5–1.5 mm thick (dry), the male flowers usually in 6 ranks, of ca. 20 flowers each (ca. 70 flowers per internode), the paired scale leaves almost completely united and only slightly cleft, 2–2.5 mm broad at the apex; female spikes with 2–5 fertile internodes, female flowers usually in 4 ranks of 2–4 flowers with 2 alternate distal flowers, ca. 10–20 flowers per internode, the united scale leaves becoming slightly cleft. Fruit ovoid to globose, 3–4 mm long, white but becoming orange in the sun, flesh translucent orange.

Branch parasites of wet evergreen and partially deciduous forest formations between (300) 1,000 and 2,000 m elevation and only rarely collected on the Caribbean slope; apparently flowering throughout the year. As here defined, the species is endemic to the area between Tilaran, Guanacaste, and western Panama (see below).

*Phoradendron tonduzii* can often be recognized almost immediately because of the long and very narrow curved leaves. The young stems with two opposite ridges, lack of scale leaves on the percurrent stems, and male spikes more slender and

with many more flowers than the female further distinguish this species. Among our species, the relationships of *P. tonduzii* are with *P. corynarthron* and *P. quadrangulare*. A number of collections from Tilaran may represent an unusual population of *P. tonduzii* (Kuijt, 1964) or a population of hybrid origin. However, these plants are here keyed to and discussed under *P. quadrangulare*. Recently, *P. tonduzii* has been placed into synonymy under *P. angustifolium*; see the discussion under that species.

**Phoradendron undulatum** Eichler, Fl. Brasil. 5, pt. 2:122. 1868. *P. gracilispicum* Trel., Gen. Phorad. 130. 1916. Figure 10.

Shrubs, often pendent, bisexual, leafy internodes 1–9 cm long, 2–8 mm thick, with 2 opposite ridges and somewhat flattened in early stages but becoming terete, percurrent stems without paired scale leaves, first lateral internodes with (1) 2 or 3 pairs of scale leaves with the distal often in the middle of the internode. Leaves opposite, articulate at the base, often slightly asymmetric, petioles 2–10 (16) mm long, with lateral ridges continuous with the lamina margins; laminae 5–17 (23) cm long, 1.5–4.5 (6) cm broad, lanceolate to very narrowly elliptic-ovate or narrowly elliptic, tapering very gradually to the acute to acuminate apex, abruptly to gradually narrowed at the obtuse to acute base, margin entire or undulate when dry, the lamininae drying stiffly coriaceous, venation pinnate with 2 or 3 pairs of major secondary veins but the secondaries often obscure. Inflorescences 1 or 2 (3 or 4) in leaf axils (2–8 per node), spikes 1.4–5 (7) cm long, with 6–12 fertile internodes 4–10 mm long, with 4 (–6) longitudinal ranks of 1–3 (4) flowers each, with usually 10–14 flowers per internode, terminal internode usually with only 2 flowers; male flowers few and usually in an apical position, pairs of fertile scale leaves often forming a distal edge perpendicular to the rachis and very slightly erose. Fruit a white globose berry ca. 4 mm in diameter, often drying cylindrical, flesh transparent and viscid.

Branch parasites of wet evergreen montane forest formations between (900) 1,100 and 2,500 m elevation in Costa Rica; probably flowering throughout the year, but collected most often in December and February. The species ranges from the Cordillera Central de Nicaragua southward to Bolivia and Brazil.

*Phoradendron undulatum* is recognized by the lack of scale leaves above percurrent internodes, flattened young stems, stiff leaves gradually tapering to the apex and with pinnate venation, spikes with short and few-flowered internodes, and the montane habitat. Small plants of *P. undulatum* are easily confused with *P. piperoides*, but that species has paired scale leaves on the percurrent internodes.

**Phoradendron sp. aff. undulatum.** Figure 10.

Shrubs, green, apparently unisexual, branches to ca. 1 m long, leafy internodes 2–5 (7) cm long, 1.5–6 mm thick, often with 2 longitudinal ridges and somewhat flattened or even quadrangular, older nodes conspicuously thickened, percurrent stems lacking scale leaves, lateral stems with 1 (rarely 2) pair of united scale leaves 8–30 mm above the branching node. Leaves usually symmetrical, petiole 5–15 mm long but gradually expanding into the leaf with lateral margins continuous with the lamina margins; laminae 5–11 cm long, 2–4 cm broad, lanceolate to narrowly ovate, tapering gradually to the acute or acuminate apex, gradually or abruptly narrowed to the attenuate base, the larger laminae more abruptly narrowed and somewhat asymmetric at the base, the lamininae drying thin to rigid-coriaceous with the margin often becoming undulate, venation palmate with usually 5 major veins, the venation often obscure. Inflorescences 1–3 from the leaf axils (2–6 per node), 2–3 cm long; male spikes with 2–5 fertile internodes, each fertile internode with 6 longitudinal ranks of ca. 4 or 5 flowers each; female spikes with 3 or 4 fertile internodes, sterile rachis of the fertile internode often as long (2–4 mm) as the fertile rachis, sterile rachis 0.6–1 mm thick (dry), female flowers in 6 ranks (4 plus 2) of only 1 or 2 flowers each. Fruit not seen.

Branch parasites of wet evergreen montane forest formations between about 2,000 and 3,000 m elevation; probably flowering throughout the year. The species is known only from the Central Volcanic Highlands and Cordillera de Talamanca in Costa Rica.

*Phoradendron* species (aff. *undulatum*) is recognized by the paired scale leaves about halfway up the first lateral internodes (to the first leaves), angular stems, acute to acuminate laminae, short spikes, and few-flowered female internodes. The description of female spikes is based on *Kuijt* 2469; no other female material is known. This species is very similar in overall appearance to *P. undulatum*, but that species has leaves with pinnate venation, more scale leaves on the lateral stems above a branching node, and undulating leaf margins.

## ARISTOLOCHIACEAE

By Kerry Barringer

REFERENCES: F. C. Hoehne, Aristolochiaceae, in *Fl. Brasil.* 15(2):1–141. 1942. Howard W. Pfeifer, Revision of the North and Central American hexandrous species of *Aristolochia*. *Ann. Missouri Bot. Gard.* 53:115–196. 1966. O. C. Schmidt, Aristolochiaceae, in Engler & Prantl, *Nat. Pflanzenfam.* ed. 2. 16b:202–242. 1935.

Lianas, herbs, or shrubs, often aromatic, wood with broad medullary rays; true stipules absent, clasping pseudostipules sometimes present. Leaves alternate, simple, petiolate; lamina entire or lobed, usually cordate and reniform, often palmately veined, often with eglandular pubescence. Flowers solitary or racemose, bisexual; calyx enlarged, petaloid, usually tubular, radially or bilaterally symmetrical, the lobes valvate; petals usually absent or reduced to scales; stamens 5, 6, or multiples thereof, free or connate, anthers extrorse, dehiscent by longitudinal slits; ovary inferior or half inferior, 4- to 6-locular, rarely of free carpels; ovules many in each locule, axile or parietal, anatropous. Fruit a septicidal capsule or follicle, usually pendent, rarely indehiscent; seeds with copious endosperm.

A family of seven genera and about 600 species, the Aristolochiaceae previously were placed in an order with the Rafflesiaceae and Hydnoraceae. They are now generally classified into an order by themselves and are believed to be derived from the Magnoliales, with affinities to the Annonaceae. Many authors have noted the similarities between the lianoid species of this family and the Dioscoreaceae. Only *Aristolochia* has been found in Costa Rica.

## ARISTOLOCHIA Linnaeus

Woody or herbaceous lianas, rarely shrubs or trees; true stipules absent but broad, clasping pseudostipules formed by the first leaf of axillary buds often present. Leaves alternate, distichous, simple, petiolate, entire or lobed, usually palmately veined with 3–7 primary veins. Flowers solitary and axillary or in racemose clusters which may be axillary or from older parts of the stem, bisexual, variously colored with yellow, brown, and red, often fetid smelling; calyx tubular, bilaterally symmetrical due to bending of the tube, forming an inflated, ovoid utricle at its base, a narrowed or funnel-form tube, and an expanded, 1- to 3-lobed, variously structured limb; stamens in multiples of 3 or 5, connate into a gynostemium which appears to also function as stigmas; ovary inferior, narrowly cylindric, 5- or 6-loculate. Fruit a dry, septicidal capsule, pendent; valves and pedicels usually splitting from the base of the capsule, the valves remaining attached at the apex, sometimes with persistent, lattice-like septa connecting the valves; seeds compressed, often with paired, lateral wings.

A genus of 400 to 500 species, chiefly pantropical. The Costa Rican species are all lianas whose flowers have six stamens and six-loculate ovaries. Little is known about the pollination of *Aristolochia* in the wild. Recent work in Costa Rica indi-



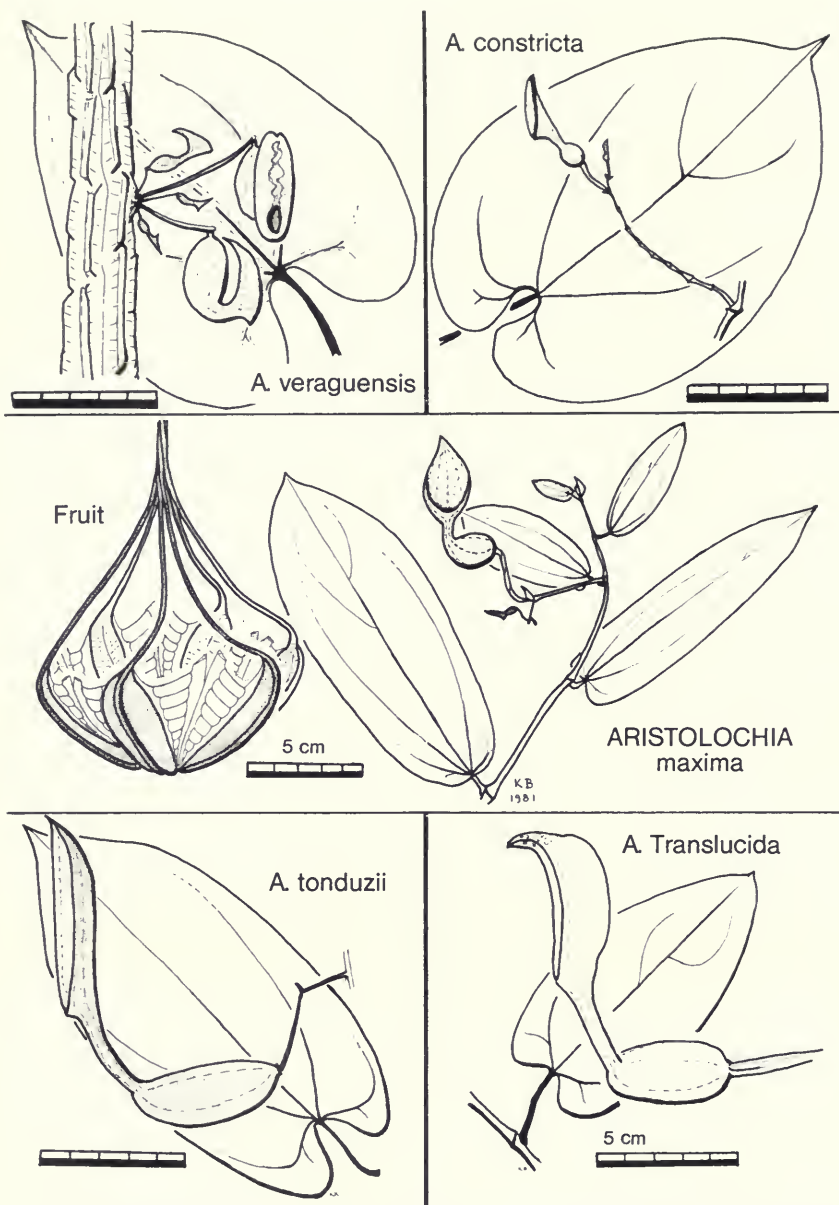


FIG. 12a. Aristolochiaceae: *Aristolochia maxima* and its Costa Rican allies; note the unusual fruit.

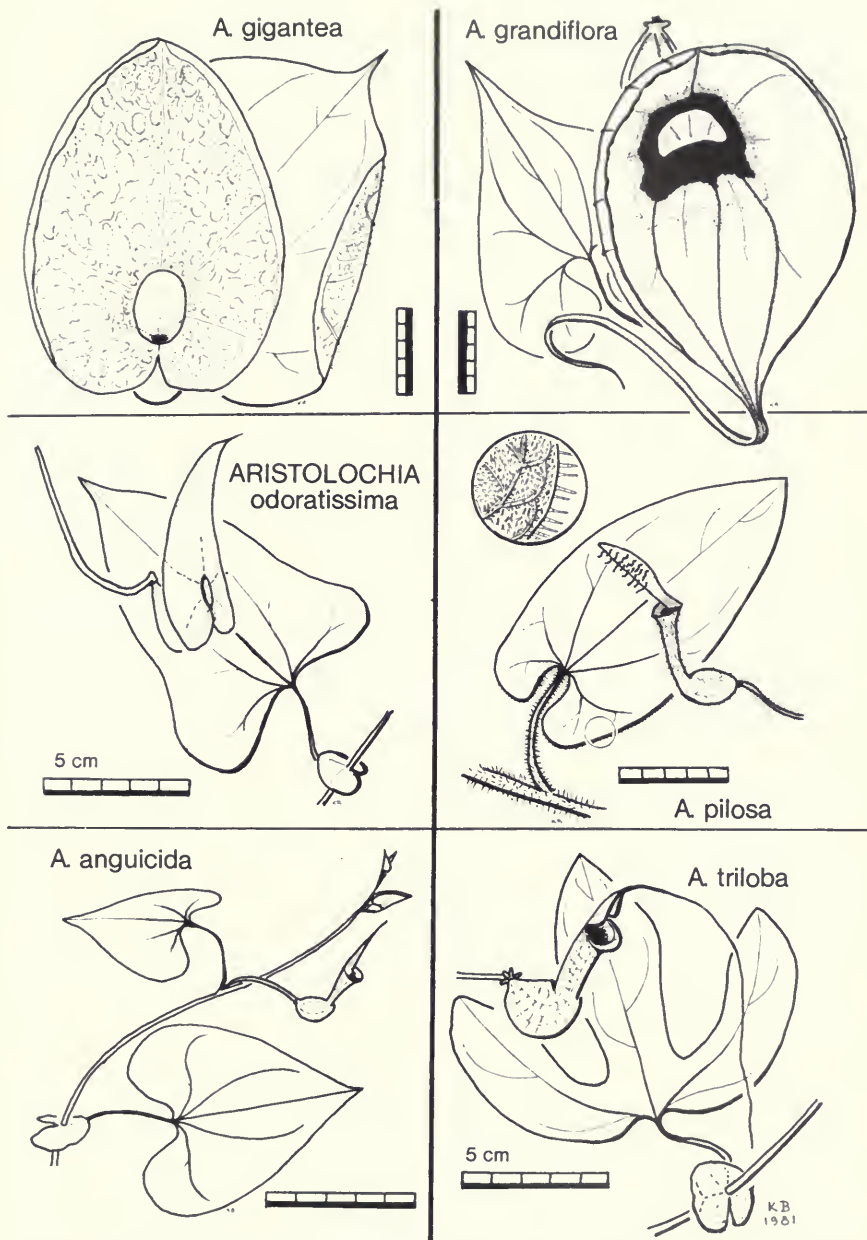


FIG. 12b. Aristolochiaceae: six Costa Rican species of *Aristolochia*, two with large flowers.

cates that butterfly larvae feed on the leaves of some species, thereby obtaining substances which make them distasteful to predators. Extracts of the stems and roots have been used against snakebite and to alleviate pain during childbirth. Sterile material is sometimes confused with species of *Dioscorea*, but *Aristolochia* can usually be recognized by the distichous leaf arrangement on young shoots.

- 1a Pseudostipules rounded, clasping, at the base of leaves ..... 2
- 1b Pseudostipules absent ..... 6
  - 2a Leaves 3-lobed; calyx limb with a long apical appendage ..... *A. trilobata*
  - 2b Leaves entire; calyx limb without apical appendage ..... 3
  - 3a Leaf blade broadly reniform, glaucous below; flowers bilabiate .... *A. ringens*
  - 3b Leaf blade triangulate, glabrous or slightly pubescent below; flowers unilabiate ..... 4
  - 4a Leaf apex rounded; fruit with a prominent beak ..... *A. littoralis*
  - 4b Leaf apex acute to cuspidate; fruit without beak ..... 5
  - 5a Capsule narrowly cylindric, 7–10 cm long; calyx limb peltate, acuminate; leaves usually hastate ..... *A. odoratissima*
  - 5b Capsule ovoid, 2–3 cm long; calyx limb triangulate, folded; leaves triangulate ..... *A. anguicida*
- 6a Plants hirsute with brown septate hairs ..... *A. pilosa*
- 6b Plants glabrous, strigose, or tomentose with white hairs ..... 7
- 7a Leaves broadest at base; fruit valves free ..... 8
- 7b Leaves broadest at middle; fruit valves usually connected by the persistent, lattice-like septa ..... 12
  - 8a Petioles 10–15 cm long ..... 9
  - 8b Petioles 2–8 cm long ..... 10
- 9a Leaves variegated with yellow or white along veins; flowers in racemose clusters on old wood ..... *A. veraguensis*
- 9b Leaves green, not variegated. Flowers solitary on older stems ..... *A. grandiflora*
  - 10a Lower leaf surface white tomentose; petioles 5–7 cm long ..... *A. gigantea*
  - 10b Lower leaf surface glabrous; petioles 2–4 cm long ..... 11
  - 11a Capsule narrowly cylindric, 7–10 cm long; calyx limb peltate, acuminate; leaves usually hastate ..... *A. odoratissima*
  - 11b Capsule ovoid, 2–3 cm long; calyx limb triangulate, folded; leaves triangulate ..... *A. anguicida*
- 12a Leaves ovate, long acuminate, deeply cordate; fruits 5–6 cm long .... *A. constricta*
- 12b Leaves oblong, short acuminate to cuspidate, truncate to shallowly cordate; fruits 6–10 cm long ..... 13
- 13a Leaf base truncate; calyx 5–7 cm long ..... *A. maxima*
- 13b Leaf base shallowly cordate; calyx 8–13 cm long ..... 14
- 14a Calyx limb translucent, with green spots ..... *A. translucida*
- 14b Calyx limb opaque, with dark elevated maculae ..... *A. tonduzii*

***Aristolochia anguicida*** Jacq., Enum. Syst. Pl. 30. 1760. *A. loriflora* Mast., Bot. Jahrb. Syst. 8(1):220. 1887. Figure 12b.

Herbaceous lianas, younger stems glabrous; pseudostipules often present, rounded, clasping, 1.5–2 cm wide. Leaves with petioles 3–4 cm long; laminae triangulate, 5–6.5 cm long, 4.5–6 cm wide, acuminate, base cordate with a sinus ca. 1 cm deep, 5 primary veins diverging from the base, glabrous. Flowers solitary in leaf axils or on short leafy shoots, ovary and pedicel 2.5–3 cm long; utricle horizontal, ovoid, 8–12 mm long, 5–7 mm wide; tube erect, funnelliform, 15–25 mm long, limb erect, unilabiate, triangulate, folded, 15–25 mm long. Capsule ovoid, 2–3 cm long, valves 6–8 mm wide, horizontally striate, finely pubescent; seeds triangulate, bilaterally winged, 6 mm long, 4 mm wide.

This species is found along the seasonally dry Pacific slope of Costa Rica and into the Meseta Central. It occurs in similar habitats from Peru to Guatemala. Flowering material has been collected from December through March, but it probably blooms throughout the year. The flowers are similar to those of *A. linearifolia*, a native of Haiti, and of *A. bilabiata* of the Greater Antilles.

***Aristolochia constricta*** Griseb., Abh. Königl. Ges. Wiss. Göttingen 7:225. 1857. *A. securidata* Mast., Bot. Gaz. 33:256. 1902. Figure 12a.

Woody lianas, older stems with ridged, corky bark, younger stems glabrescent; pseudostipules absent. Leaves with petioles 3–5 cm long; laminae ovate, 10–20 cm long, 7–13 cm wide, long acuminate, bases deeply cordate with sinuses 2–4 cm deep, 5 primary veins diverging from the base, glabrous above, glabrescent below. Flowers in axillary racemes; utricle horizontal, ovoid, 1 cm long; tube erect, funnelform, 2 cm long; limb erect, unilabiate, 2–3 cm long. Capsules broadly ellipsoid, 5–6 cm long, valves 2 cm wide, horizontally striate, glabrous, septa persistent, lattice-like, connecting the valves after dehiscence; seed cordate, with broad lateral wings, 7 mm long, 12 mm wide.

Native to Costa Rica, northern Panama, and southern Nicaragua, growing in evergreen forests below 1,000 m. Flowering material collected between October and May.

This species can be recognized by its ovate, long-acuminate, deeply cordate, glabrous leaves. The species seems to be closely related to *A. maxima*. The fruits have persistent septa which connect the valves of the fruit after dehiscence, making the fruit look like a hanging basket. Similar fruits are found in *A. maxima*, *A. chapmaniana*, *A. tonduzii*, and probably *A. translucida*.

***Aristolochia gigantea*** Mart. & Zucc., Nov. Gen. Sp. Pl. 1:75. t. 48. 1824. *A. sylvicola* Standley, J. Wash. Acad. Sci. 15:5. 1925. Figure 12b.

Woody lianas, older stems with a deeply ridged, corky bark, younger stems glabrous; pseudostipules absent. Leaves with petioles 5–7 cm long; laminae ovate to triangular, 15–16 cm long, 11–16 cm wide, apices acuminate, bases truncate to slightly cordate, with 5 major veins diverging from the base, glabrous above, villous with white hairs below. Flowers borne on older stems; utricle pendent, turbinate, 7 cm long, 3 cm wide; tube strongly reflexed, funnelform, 3 cm long, limb erect, peltate, 15–17 cm long, 12–13 cm wide, with purple-brown markings between the veins. Capsule cylindric, 13 cm long, valves 8–10 mm wide, glabrous, horizontally striate; seeds ovate, without wings, 7 mm long, 5 mm wide.

Currently known from the wet lowland forests from Panama to Amazonian Brazil; it is likely that this species will be found in Costa Rica. Flowering material has been collected from September to March.

This species can be recognized by the leaves, which are villous on the lower surface, and the broadly peltate calyx limb. The Central American material differs from the South American material in having smaller flowers, no pseudostipules, and white hairs on the lower leaf surface. The two groups may be distinct taxa, but these characters are known to vary within some species. *Aristolochia gigantea* is closely related to *A. littoralis*.

***Aristolochia grandiflora*** Swartz, Prodr. Veg. Ind. Occ. 126. 1788. Figure 12b.

Lianas, older stems with a corky bark, younger stems glabrous; pseudostipules absent. Leaves with petioles 10–17 cm long; laminae triangulate, 8–15 cm long, 9–17 cm wide, apices acute, bases deeply cordate with sinuses 3–6 cm deep, glabrous. Flowers solitary on older stems, fetid; utricle pendent, narrowly ellipsoid, 9–11 cm long, with prominent veins, tube strongly bent, 2–3 cm long, bullate at base of limb, limb funnelform, pendent, 15–20 cm long, with a long caudate appendage to 1 m long at its apex, veins prominent, purple-brown on veins within. Capsule cylindric, 10 cm long; seeds triangulate.

Common in wet lowland forests below 1,000 m along both coasts. Plants have been cultivated in San Jose. The species is found from Mexico to Panama and throughout the West Indies.



The leaves of this species resemble those of *A. veraguensis*, but are not variegated. The flowers are among the largest of any neotropical plant and are extremely fetid. The flowers are distinctive because of their size and because of the long apical appendage.

***Aristolochia littoralis*** Parodi, *Anales Soc. Ci. Argent.* 5:155. 1878. *A. elegans* Mast., *Gard. Chron.* n.s. 34:301. t. 61. 1885.

Lianas, older stem with a ridged bark, younger stems glabrous; pseudostipules rounded, clasping, 1.5–2.5 cm wide. Leaves glabrous, petioles 3–5 cm long; laminae triangulate, broader than long, 3–5 cm long, 4–6 cm wide, apex rounded, base cordate with a sinus 1 cm deep, 5 primary nerves diverging from the base. Flowers solitary in leaf axils; utricle horizontal, oblong, 3.5 cm long, tube erect, 3 cm long, limb erect, peltate, 10 cm long. Capsule ellipsoid, 4–5 cm long, with a 6 mm long beak at its apex, valves 4–5 mm wide, horizontally striate, glabrous; seeds triangulate, slightly winged, 5–6 mm long, 4–5 mm wide.

Native to South America, widely cultivated and escaped in Central America. The species flowers through most of the year and appears to set viable seed without insect pollinators.

This species can be recognized by the triangulate leaves with pseudostipules and the peltate calyx limb. It is similar to *A. gigantea* in the structure of the flowers, but the flowers of *A. gigantea* are much larger. The fruit is distinctive due to the short beak at its apex.

***Aristolochia maxima*** Jacq., *Enum. Syst. Pl.* 30. 1760. *Howardia hoffmanni* Klotzsch, *Aristoloch. Berl. Herb.* 621. 1859. *A. maxima* var. *angustifolia* Duchartre, in DC., *Prodr.* 15(1):457. 1864. Figure 12a.

Woody lianas, older stems with a deeply ridged, corky bark, younger stems glabrescent with strigose hairs; pseudostipules absent. Leaves with petioles 1–2 cm long; laminae oblong to obovate, 7–15 cm long, 3–7 cm wide, apices acuminate, base truncate to slightly cordate, glabrous above, glabrescent beneath. Flowers in loosely branched rhipidia from the axils of leaves or from the base of the stem; ovary and pedicel 3 cm long, utricle horizontal, ovoid, 2–3 cm long, 1 cm wide, tube bent, funnelform, 2 cm long, limb erect, unilabiate, ovate, slightly hooded, 3–5 cm long, purple-brown. Capsule ovoid, 10–15 cm long, valves 2 cm wide, glabrous, held together after dehiscence by persistent, lattice-like septa; seed triangulate, winged, 1 cm long, 1.5 cm wide.

In thickets and forests along both coasts below 1,000 m and rarely found in the Meseta Central, where it may have escaped from cultivation. The species is found throughout Central America and into Colombia and Venezuela.

The species can be recognized by the oblong leaves which are glabrous when mature and which usually have truncate bases. The inflorescences are unusual in the genus, not only because of their branching pattern, but also because they may appear from the base of the plant. The species is closely related to *A. bicolor* of Colombia. Pittier reported that the young fruits are edible.

***Aristolochia odoratissima*** L., *Sp. Pl.* 1362. 1763. *A. pandurata* Jacq., *Pl. Hort. Schoenbr.* 4:49. t. 497. 1804. Figure 12b.

Lianas, glabrous; pseudostipules rarely present, 1–2 cm wide, clasping. Leaves with petioles 4 cm long; laminae hastate-triangulate, 10–15 cm long, 8–10 cm wide, apices acute, bases cordate with a sinus 5–15 mm deep, with 3 major veins diverging from the base, glabrous. Flowers solitary in leaf axils; ovary and pedicel 6–7 cm long, utricle pendent, ovoid, 2–3 cm long, 1 cm wide, tube erect, 1–2 cm long, expanding slightly

above, limb erect, unilabiate, peltate, 5–10 cm long, 3–5 cm wide, acuminate, dark purple-brown. Capsule narrowly cylindric, curved, valves 5 mm wide, glabrous; seeds rhombic to triangulate, without wings, 3 mm long, 2 mm wide.

Widely distributed in wet forests throughout the neotropics. This species shows considerable geographic variation throughout its range and has been divided into many species in South America. In Costa Rica, plants have been collected near Pto. Limon where they seem to bloom throughout the year.

*Aristolochia odoratissima* can generally be recognized by the hastate leaves, but in cases where the leaf shape is variable, the peltate and acuminate calyx limb is distinctive. It is related to the other *Aristolochia* species with peltate calyx limbs, including *A. gigantea* and *A. littoralis*.

***Aristolochia pilosa*** H.B.K., Nov. Gen. & Sp. 2:146. t. 113. 1817. *Howardia costaricensis* Klotzsch, Aristoloch. Berl. Herb. 614. 1859. *A. costaricensis* (Klotzsch) Duchartre, in DC., Prodr. 15(1):450. 1864. *A. costaricensis* var. *zamorensis* Heiron., Bot. Jahrb. Syst. 20(Beibl. 49):5. 1895. Figure 12b.

Lianas, all parts hirsute with brown, septate hairs, older stems with a deeply ridged, corky bark; pseudostipules absent. Leaves with petioles 3–7 cm long; laminae deltoid to ovate, 10–14 cm long, 8–10 cm wide, apices acute to rounded, margins ciliate, bases deeply cordate with sinuses 1–3 cm deep, glabrous above, hirsute on veins and white pubescent on areolae below. Flowers solitary in leaf axils; pedicel and ovary to 6 cm long, utricle horizontal, ovoid, 15–20 mm long, 10–12 mm wide, tube erect, 15–25 mm long, flaring slightly at mouth, limb erect, unilabiate, ligulate, 30–40 mm long, 15–25 mm wide, fimbriate to efimbriate, maculate. Capsules broadly ellipsoid, 5–7 cm long, valves 5 mm wide; seeds obovate, acute, without wings, 4 mm long, 3 mm wide.

Plants of the wet lowlands on the Atlantic coast and the Osa Peninsula, from sea level to 850 m elevation. Probably blooming throughout the year. This species is distributed in wet forests from southern Mexico to the Amazon.

*Aristolochia pilosa* is easily recognized by the conspicuous brown pubescence on most of the plant; it is variable in leaf shape and in the pigmentation and vestiture of the limb. Closer study of the species throughout its range may show it to be a group of closely related species.

***Aristolochia ringens*** Vahl, Symb. Bot. 3:93. 1794.

Woody lianas, older stems with a ridged, corky bark, younger stems glaucous; pseudostipules rounded, clasping, 2–3 cm wide. Leaves with petioles 10–11 cm long, glaucous; laminae broadly reniform, 9–10 cm long, 13–15 cm wide, apex rounded, base deeply cordate with a sinus 3 cm deep, glaucous, with 7 primary veins diverging from the base. Flowers solitary in leaf axils; utricle pendent, turbinate, 5–6 cm long, tube bent, funnelform, 2–2.5 cm long, limb horizontal, bilabiate, the upper lobe spatulate, 8 cm long, the lower lobe lanceolate, 8–9 cm long, 2–3 cm wide. Capsules cylindric, 8 cm long, glaucous; seeds cordate, bilaterally winged, 12 mm long, 7 mm wide.

Native to South America and widely cultivated in tropical and subtropical areas. In Costa Rica, plants have been grown in San Jose. It is the only bilabiate species known from Costa Rica and can be recognized by the broad reniform leaves and pseudostipules. The bilabiate aristolochias are a distinctive group within the genus; their taxonomy has yet to be satisfactorily worked out.

***Aristolochia tonduzii*** Schmidt, Repert. Sp. Nov. 23:284. 1927. *A. chapmaniana* Standley, Contr. Arnold Arbor. 5:60. 1933. Figure 12a.

Woody lianas, older stems with a ridged, corky bark, younger stems glabrescent, strigose; pseudostipules absent. Leaves with petioles 1.5–3 cm long, strigose hairy; laminae ovate to oblong, 10–16 cm long, 4–8 cm wide, short acuminate, bases cordate with a sinus 5–20 mm deep, glabrous above, densely strigose below. Flowers racemose on short axillary branches; ovary and pedicel 2–3 cm long, strigose, utricle horizontal, ellipsoid, 3–4 cm long, 1.5 cm wide, strigose, tube slightly bent, 1.5–3.3 cm long, strigose, flaring at mouth, limb erect, unilabiate, hooded or folded back, 4–6 cm long, 1–2 cm wide, maculate on inner surface, purple. Capsule ovoid, 10 cm long, valves 2 cm wide, held together after dehiscence by persistent, lattice-like septa; seeds deltoid, cordate, 9 mm long, 15 mm wide, winged.

This species is found in the wet lowland forests of the Atlantic coast. Flowering specimens have been collected from April through July, and fruiting specimens have been collected throughout the year.

The cordate leaf base and strigose lower leaf surface distinguish *A. tonduzii* from *A. maxima*. The flowers of *A. tonduzii* are also larger, and the inflorescence is not as strongly branched. *Aristolochia tonduzii* is very closely related to *A. schmidtiana*, native to Amazonian Peru.

***Aristolochia translucida*** H. W. Pfeifer, Brittonia 28(3):349. 1976. Figure 12a.

Woody lianas, older stems with a ridged, corky bark, young stems strigose; pseudostipules absent. Leaves with petioles 2 cm long; laminae oblong-ovate, 10 cm long, 5 cm wide, apices slightly acuminate, bases cordate with sinuses to 1 cm deep, with 3 major veins diverging from the base, glabrous above, strigose below. Flowers on short axillary branches; pedicel and ovary to 4 cm long, utricle horizontal, ovoid, 4 cm long, tube erect, funnellform, 2 cm long, limb unilabiate, hooded, translucent, 8–9 cm long, with elevated green maculae within. Fruit and seed unknown.

Known only from the type collection, found growing at "La Selva" in the Caribbean lowlands near Puerto Viejo de Sarapiquí. Living material was collected without flowers and bloomed later in a northern greenhouse. *Aristolochia translucida* is very similar to *A. tonduzii*, differing chiefly in the pigmentation of the flowers. More collections are needed to determine the variability and range of this species.

***Aristolochia trilobata*** L., Sp. Pl. 960. 1753. Figure 12b.

Woody lianas, young stems glabrous; pseudostipules rounded, clasping, 1–2.5 cm wide. Leaves with petioles 3 cm long; laminae 3-lobed, 7–9 cm long, 7–11 cm wide overall, the middle lobe 2.5–3.5 cm wide, apex acute to rounded, base truncate to slightly cordate, glabrous. Flowers solitary in leaf axils; ovary and pedicel to 6 cm long, utricle horizontal, ovoid, 3 cm long, with a 6-lobed, starlike hypanthium at its base, tube bent, erect, 2 cm long, limb unilabiate, triangulate, 1.5 cm wide, with a long, pendent, caudate apex, over 15 cm long. Capsule ovoid, 5 cm long, valves 1.5–2 cm wide, glabrous, horizontally striate; seeds triangulate, bilaterally winged, 8 mm wide, 8 mm long.

A circumcaribbean species found in lowland woods and thickets on the Atlantic coast. In Costa Rica, the species has been found near Limón. This is the only Costa Rican species which has lobed leaves. Its relationships are obscure, but it is most likely not closely related to the other Caribbean species with lobed leaves.

***Aristolochia veraguensis*** Duchartre, in DC., Prodr. 15(1):458. 1864. Figure 12b.

Woody lianas, older stems with ridged, corky bark, to 10 cm diameter, younger stems glabrous; pseudostipules absent. Leaves with petioles 10–12 cm long; laminae variegated with white or yellow along veins, triangulate, 13–17 cm long, 13–15 cm wide, acuminate, deeply cordate, with a sinus 3–4 cm deep, glabrous. Flowers in dense, racemose clusters

on older stems; ovary and pedicel 5–6 cm long; utricle pendent, ovoid, 1.5–2 cm long, 1 cm wide, tube strongly bent, 1–1.5 cm long, limb funnellform, 2.5–3.5 cm long, acute, yellow with purple marking around the edge. Capsule cylindric, 14–20 cm long, valves 5 mm wide, glabrous; seeds ovate, without wings, 3 mm long, 1 mm wide.

Plants of the seasonally dry, lowland forest in Guanacaste, Puntarenas, and San Jose. Generally found below 1,000 m, but cultivated at higher elevations. Also known from Panama. The plants bloom from December to May. This species is very distinctive due to its variegated leaves. It is probably related to *A. schippii* of southern Mexico and Belize.

## HYDNORACEAE

By Luis D. Gómez

Parasitic plants on roots of the host, lacking chlorophyll, stems all subterranean, lacking leaves and roots, underground stem (rhizome) producing terete or 3- to 6-angled rhizoids with numerous, elongated and wartlike protuberances. Flowers solitary or groups borne on the rhizome and usually with only the distal part of the flower above the ground, large and bisexual, thick-fleshy, perianth of 1 whorl of 3 or 4 valvate sepals (tepals), the fleshy perianth united below to form a thick tube and opening distally, the perianth lobes either opening and diverging or remaining united at their tips and opening below to form a lantern-like structure; stamens borne on the perianth tube, anthers very large and numerous, united into a ringlike mass on the perianth tube or forming syndandria of tightly united undulating thecae, the syndandria as many as the perianth lobes in *Hydnora*; ovary inferior, of 3 fused carpels with a single locule containing many reduced ovules on placentas which are leaflike or lamellate, the placentation parietal or pendulous from the apex of the large locule, stigma broad and rounded or button-like, sessile. Fruit usually formed underground, a large thick-walled fleshy berry; seeds minute, with copious endosperm and a verrucose or pitted testa.

An unusual family of parasites with very large fleshy flowers that remain partially underground and are pollinated by beetles. The Hydnoraceae are probably most closely related to the Rafflesiaceae and Balanophoraceae from which they differ in the bisexual flowers. *Hydnora*, with some six to 10 species in Africa and Madagascar, and *Prosopanche*, with two species in southern South America and a newly discovered species in Central America, are the only genera in the family.

## PROSOPANCHE DeBary

REFERENCE: A. E. Cocucci, Estudios en el género *Prosopanche* 1. Revisión taxonómica. Kurtziana 2:53–74. 1965.

Herbs, completely parasitic, vegetative stem hypogean, a thick mass of tissue from which arise the flowers which are its only aerial parts and long underground 4- to 5- (6-) angled rhizoids bearing numerous wartlike haustorial rudiments on the aristae. Leaves absent. Flowers bisexual, perianth fused at the base to form a tube of variable length, the upper edge of which subtends the stamens, tepals (perianth lobes) 3, thick and valvate; stamens 3, opposite the tepals, filaments much reduced, more or less deltoid and fused to the perianth tube on one side and with an anther at the distal end, anthers with 15–30 thecae concrescent to form a conical or ovoid syndandrium, dehiscing longitudinally, ex-torse; an inner whorl of 3 bilobed interstaminal appendages alternating with the stamens; pistil 1 and united with the perianth tube, ovary inferior, 3 carpellate, the solitary locule completely filled by numerous lamellar parietal placentae the upper ends of which are united to form a button-like stigmatic surface which plugs the upper end of the locule, the ovules very reduced, embedded in the placental walls, absent near the stigmatic surface. Fruit a fleshy berry; seeds numerous, small, with pitted or verrucose episperm, dark brown or black at maturity, very hard.



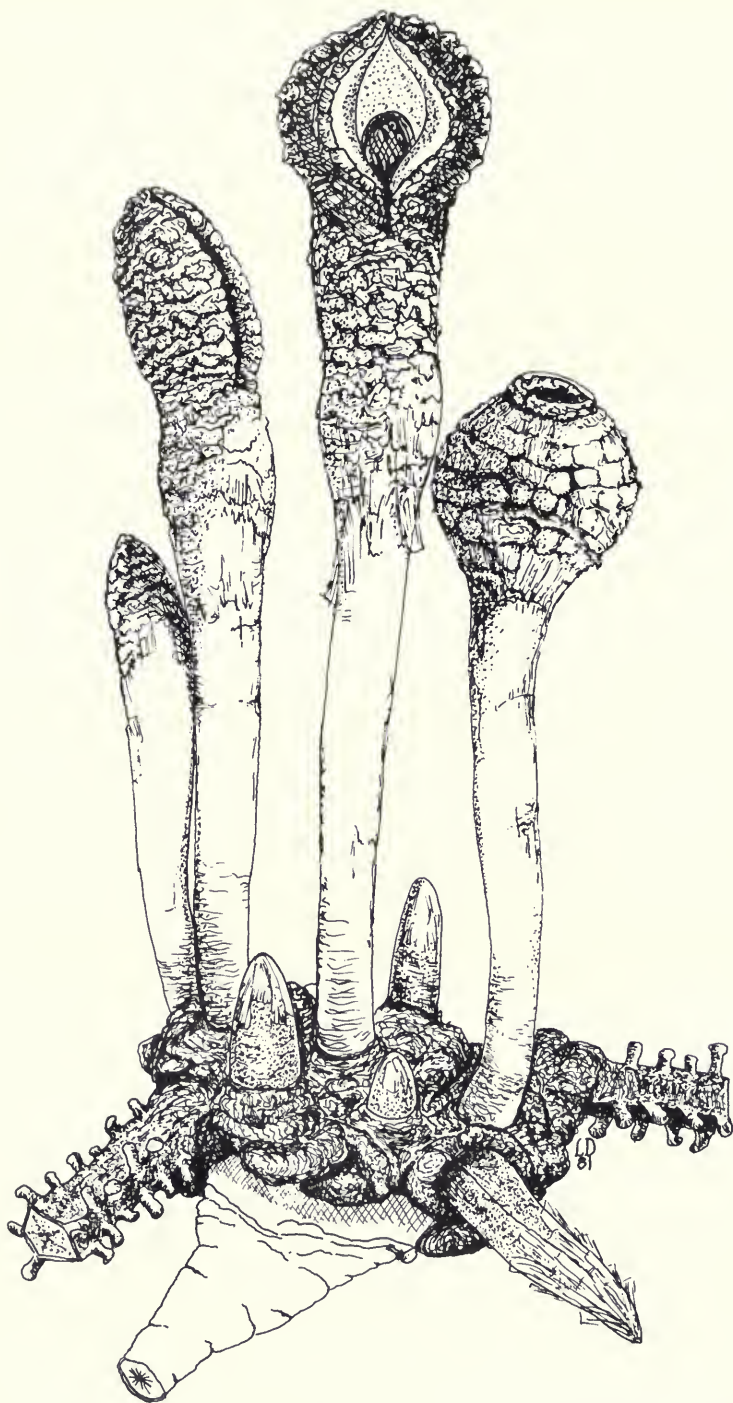


FIG. 13. Hydnoraceae. *Prosopanche costaricensis*; vertical scale at the right is 5 cm high.

The genus is represented by *P. americana* (R. Br.) Baillon, which is parasitic on Leguminosae, mainly *Prosopis*, and *P. bonacinae* Spegazzini, which parasitizes several dicotyledonous families. Both species are found only in the drier parts of southern South America. *Prosopanche costaricensis* is the only species known from Central America and northern South America.

***Prosopanche costaricensis*** Gomez & Gomez-L., *Phytologia* 49:53. 1981. Figure 13.

Thick-fleshy herbs, found in clumps forming extensive colonies, parasitizing the roots of leguminous trees, rhizoids 4- or 5-angular, up to 15 mm thick, with numerous fragile haustorial rudiments. Flowers pedicellate, pedicels up to 150 mm long and 15 mm thick, the flowers averaging ca. 6 cm long and 2 cm thick when in bud, sepals 3, up to 90 mm long and 35–42 mm broad, externally flocose or with lenticel-like warts, inside smooth and white, valvate and remaining joined at the tip with the perianth segments forming a narrow lantern-like structure when open, perianth tube short (ca. 7 mm), the exterior diameter 25–32 mm; synandrium conical, 19–23 (29) mm long, 11–22 mm broad at the widest point, anthers white when young, dark brown or black when mature, thecae ca. 25, dehiscing longitudinally; ovary ca. 50–60 mm long and 40–53 mm in external diameter when mature, also flocose-warty on the exterior, stigmatic surface 3-radiate with fewer than 12 pairs of lamellae lobes in frontal view. Seeds elliptic, 1–1.3 mm long, 0.6–0.7 mm wide, buff when young, black in maturity, testa rugulose-verrucose.

This species is known only from cacao groves near Siquirres at about 50 m elevation at the edge of the Caribbean coastal plain in evergreen wet forest formations. The plants are parasitic on *Inga orstediana* and possibly *Gliricidia saepium*. Unlike its South American congeners, this plant inhabits a tropical rain forest region. Its closest affinity is with *P. americana* from which it differs in various aspects, particularly size of structures, seed ornamentation, and folds or lobes of the stigmatic surface.

*Editor's note:* The collection of *Prosopanche* by Luis D. Gómez and Jorge Gómez-Laurito in June 1981 was an exciting find. This is not only a major geographical disjunction for the genus, but a new ecological niche. The brown warty flowers are easily mistaken for stems and roots on the forest floor. Surprisingly, an earlier collection from Costa Rica in Field Museum's fruit collection had been overlooked. This specimen was collected by W. R. Hatch on July 22, 1937, identified as *Corynea crassa*, and annotated as *Prosopanche* by Bertel Hansen in 1976. The only information this collection gives us is the word *Reventazon*, a river that descends the highlands and flows close by Siquirres.

## RAFFLESIACEAE

By Luis D. Gómez

REFERENCES: J. Kuijt, *The Biology of Parasitic Flowering Plants*, Univ. of California Press, 1969; I. Vattimo, *Contribuição ao conhecimento da tribo Apodanthea R. Br. Parte 1, Conspecto das Espécies*. *Rodriguezia* 26, no. 38:37–62, 1971.

Herbaceous parasites, without chlorophyll and without roots, stems short and fleshy or absent and flowers emerging directly from the tissues of the host, borne on the aerial woody stems or on the subterranean roots of the host. Leaves absent or represented by bracts or scales. Inflorescences racemose or the flowers borne directly from the stems or the roots of the host, neotropical genera with small (less than 1 cm) to medium size (up to 3.5 cm in diameter) flowers (*Rafflesia* with the world's largest flower, ca. 1 m in diameter). Flowers radially symmetric, usually unisexual by abortion, rarely bisexual, perianth of 4–10 imbricate (rarely valvate) or spreading segments or calyx lobes, united at the base to

form a short tube; stamens 5 to many, filaments united into a tube, column or syndrium, anthers sessile, arranged in 1–3 whorls around the apex of the column or staminal tube, 1- or 2-thecous, opening by a longitudinal slit, pollen decussate, acopate or 3- or 4-colpate, without sculpturing, sometimes shed in tetrads; pistil superior to inferior, carpels 4, 6, or 8, ovary always unilocular, placentae 4, 6–20, or more, placentation parietal over the inner wall or toward the distal (apical) portion of the locule (in transection the locule appears circular, cruciform, or lamellate, with many parietal projections from the wall), ovules very numerous and sessile, stigma solitary, terminal on a slender style or stout column, capitate to discoidal, undivided or obscurely lobate. Fruit a fleshy berry with many seeds, opening irregularly, often concrescent in *Bdallophyton*; seeds very small, with a hard testa, often with few (8) cells rich in fatty substances.

This unusual family of parasites, containing about nine genera and 50 species, is well represented in the Old World, with the best known examples being *Cytinus* and *Rafflesia*. In the neotropics, the family is represented by the genera *Apodanthes* and *Pilostyles* of the Apodantheae, and *Bdallophyton* and *Mitrostemon* of the Cyttineae. *Bdallophyton* is the only genus endemic to the American tropics. The biology of the family, which is little known, has been summarized by Kuijt (1969). Plants of *Apodanthes* and *Pilostyles* are easily passed by since they appear only as small flowers on the thicker stems of the host, often only 5 mm high.

- 1a Parasites on aerial branches of Flacourtiaceae or Leguminosae; flowers solitary and terminal, subtended by a short peduncle covered by closely appressed bracts, borne directly on the stem of the host, often with scars of previous flowers evident on the bark of the host in the immediate vicinity; Apodantheae. . . . . 2a
- 1b Parasites on the horizontal roots of Burseraceae or Fagaceae; flowers several to many in racemose inflorescences; stems evident and single or branched above the tissue of the host, stems with leathery foliose or triangular bracts; Cyttineae. . . . . 3a
  - 2a Locule of ovary cruciform in transection, placentation restricted to the swollen longitudinal ribs; flowers subtended by 4 alternate bracts, exserted, 4-segmented, subepigynous, not persisting; parasites on Flacourtiaceae. . . . . *Apodanthes*
  - 2b Locule of ovary evenly circular in transection with placentation on the entire inner surface; flowers subtended by a wide base covered with imbricate bracts and concealed, parasites on Leguminosae. . . . . *Pilostyles*
- 3a Plants large, up to 25 cm tall, stems well developed and with many foliose bracts, these spirally arranged but often with the internodes so reduced as to produce bracts in pseudowhorls; flowers axillary on a racemose axis; ovary inferior; parasites on the roots of Burseraceae, *Ficus* and *Cochlospermum* . . . . . *Bdallophyton*
- 3b Plants smaller, usually 4–8 cm tall; stems not well developed and often concealed by many bracts; ovary superior or subinferior; parasitic on roots of *Quercus* and perhaps *Carpinus* (Betulaceae) . . . . . *Mitrostemon*

#### APODANTHES Poiteau

Very small plants parasitic on the aerial stems of the host (almost always species of Flacourtiaceae, especially *Casearia*), aerial stems very short (less than 5 mm), leaves reduced to small scales, only the cupular stem apex with whorled scale leaves and flower or fruit visible on the stem surface of the host. Flowers solitary from a woody cupule borne on the bark of the host (but flowers usually occurring in groups on the surface of the host), the cuplike stem apex with 3 whorls of imbricate scales, the 1st whorl with 2 free scale leaves, the 2nd with 4 scales united at the base, and the 3rd whorl with thinner rounded petal-like parts that are deciduous. Flowers unisexual, small, radially symmetrical, the male flowers with a central "stylar" column broadened and stigma-like at the top beneath which 2 series of many (ca. 20) subsessile stamens are attached; female flowers with a partly inferior ovary, 1-locular with many ovules, stylar column cylindrical and narrow above, stigma annular. Fruit baccate, subtended by the woody and scaly cup; seeds with hard testa.

Seven species have been reported for the genus, ranging from Mexico to Guatemala and Honduras, Panama, and northern South America. The Mexican plants

may all be forms of *A. caseariae* Poit., while in South America all described material may be referable to either *A. flacourtiiae* Karst. or *A. tribracteata* Rusby. Only one species is known from Costa Rica.

***Apodanthes caseariae* Poit.**, Ann. Sci. Nat. (Paris) 3:422. 1824. *A. panamensis* Vatt., nom. nud. Figure 8.

Small, leafless, parasitic herbs, emerging from bark of trunk and branches of Flacourtiaceae. Flowers solitary. Pistillate flowers white, subtended by a receptacle, 1–2 mm high and 2–3 mm wide, formed in the outer bark of the host plant; basal bracts 2, suborbicular cucullate, leathery, 2–3 mm long; the upper bracts 4, apically rounded, almost twice as long as the basal ones, fused to the lower  $\frac{1}{2}$  or  $\frac{1}{3}$  of the ovary and pressed against the ovary; calyx segments 4, obovate, imbricate, slightly inequilateral, borne in a shallow and small depression near the apex of the ovary, petals lacking; ovary ovoid, creamy white to dirty yellow to orange, 3–4 mm long; ovules numerous, parietal on folds or invaginations within the unilocular ovary, style thick, 2 mm long, dilated toward the apex, stigma finely papillate. Staminate flowers with a short stylar column which subtends 2 series of many stamens each, stamens almost sessile. Fruit a berry.

Only known from the General Valley where it grows abundantly on *Caesaria nitida*. The most evident stage is the fruit, which becomes yellow or orangish in maturity and is eaten by *Thraupis* birds. The flowers are visited by *Trigona* bees. These parasites have been reported as growing on Burseraceae and Meliaceae, in addition to Flacourtiaceae, in northern Central America. On Barro Colorado Island, Panama, these parasites have been seen only in August and September.

#### BDALLOPHYTON Eichler

This is the only genus of the Rafflesiaceae endemic to the neotropics. The plants are parasitic on the roots of Burseraceae, fleshy, with well-developed stems bearing lanceolate, acute, foliose bracts. Racemose inflorescence often producing concrescent fruit. Two species have been described: *B. americanum* (A. Br.) Harms and *B. oxylepis* (B. L. Robinson) Harms, the latter of which differs from the former only in size of plants, which are slightly smaller, and in the reduced internodes of the infructescence which give it the appearance of a small pineapple. I consider the genus as monotypic.

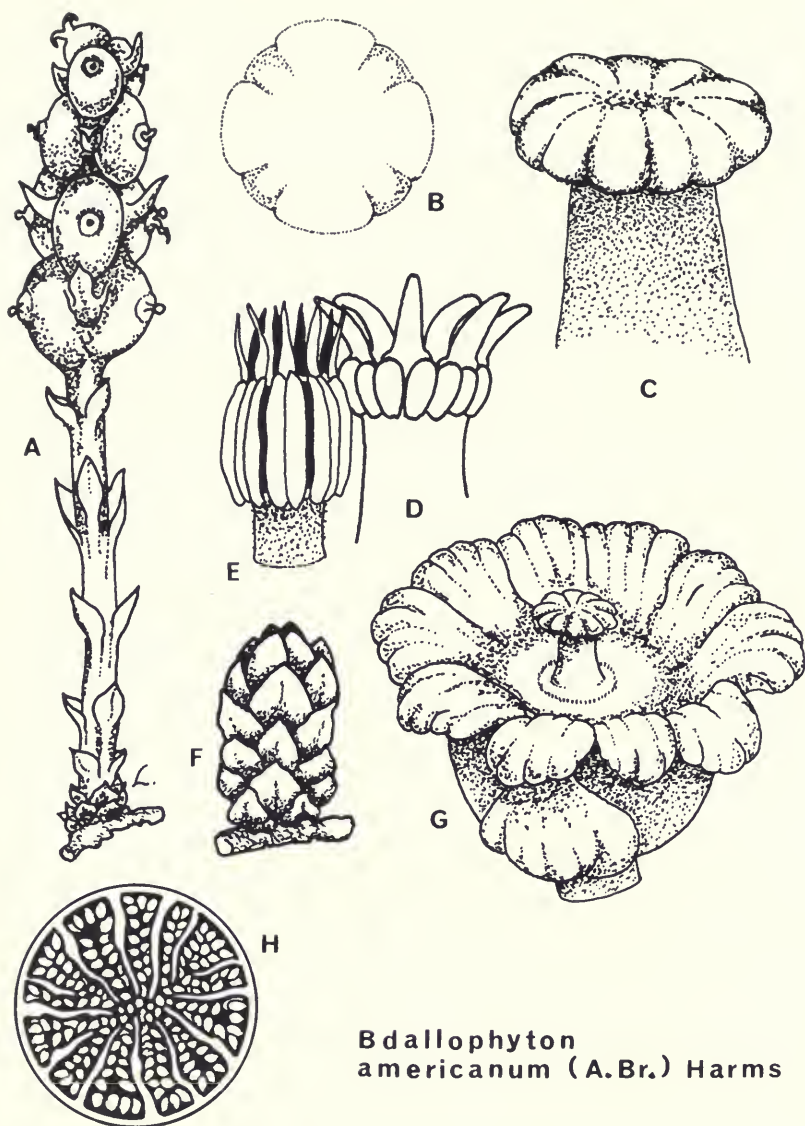
***Bdallophyton americanum* (A. Br.) Harms**, in Engler & Prantl, Nat. Pflanzenfam. ed. 2, 17b:281. 1935, based on *Cytinus americanum* R. Br., Trans. Linn. Soc. (London) 19:246. 1845. *B. andreuxii* Eichl., Bot. Zeitung. (Berlin) 39:715, t. 8B. 1872. *B. cerantantherum* Eichl. loc. cit. t. 8A, figs. 1–5. *B. bambusarum* (Liebm.) Harms, loc. cit. *B. oxylepis* (B. L. Robinson) Harms, loc. cit. Figure 14.

With characters of the genus and those given in the generic key.

Plants when alive a drab purplish olive green, the pigment dissolving in alcohol leaving all parts an opaque olive brown. Anthers sometimes relatively short and swollen or elongate and rather narrow ( $4-5 \times$  as long as wide), horny projections straight in the immature flowers, curving outward just before dehiscence of the pollen. Pollination carried out by flies, apparently attracted only by the morbid color since no odor was perceived at the time of observation. The seed are carried around by rodents, the ripe fruit often showing the signs of sharp incisors.

In Costa Rica, the plants are known only from one locality, the riparian forest along the lower course of Rio Calera, Parque Nacional Sta. Rosa, Guanacaste Province. Blooms in the months of October to early December.





***Bdallophyton*  
*americanum* (A.Br.) Harms**

FIG. 14. Rafflesiaceae. A–H, *Bdallophyton americanum*: A, habit of female plant showing concrescent fruits; B, polar view of 4-colpate pollen grain; C, discoid and lobate stigma; D, E, types of anthers and anther appendages; F, young shoot covered by imbricate bracts; G, female flower; H, diagrammatic view of transection of ovary.

## PILOSTYLES Guillemín

No representatives are so far recorded from Costa Rica, where they may occur on the Leguminosae of the tropical dry forest and at middle elevations of the northern mountain ranges of the country. *Pilostyles thurberi* A. Gray and *P. globosa* S. Watts are known from northern Central America. *Pilostyles covillei* Rose is described from Colombia. Like *Apodanthes*, these plants appear as small (5 mm) projections or pustules on the branches of the host. These projections give rise to the flowers which are often found in considerable number and give the parasitized branch a peculiar warty appearance.

## MITRASTEMON Makino

Originally described under the name *Mitrastemma*, Makino later not only changed the generic name to its present form, but also transferred the genus from Rafflesiaceae to Mitrostemonaceae (in Bot. Mag. [Tokyo] 25:253, 1911), proposing also a separate order, Mitrostemonales. Unlike all other Rafflesiaceae, *Mitrostemon* has a subinferior to superior ovary. In other characters, it conforms with the family concept. One species, *M. matudai* Yamamoto, in Matuda (Bull. Torrey Bot. Club 74:133, 1947), is described and illustrated from Mexico and Guatemala, where it is a parasite on the roots of *Quercus* (Fagaceae). It might possibly occur in Costa Rica in the same habitats as *Conopholis* (Orobanchaceae), also parasitic on *Quercus* and ranging from the central portions of Mexico southward into northern South America. *Mitrostemon matudai* is the only species in the New World; the others are from Japan, Formosa, and southeastern Asia to Borneo.

## BALANOPHORACEAE

By Luis D. Gómez

REFERENCE: B. Hansen, Balanophoraceae, Flora Neotropica, Monograph 23:1-80, 1980.

Fleshy parasitic herbs devoid of chlorophyll, consisting of a cylindrical tuberous rhizome, long-creeping and then dichotomously branching or globose and massive, epigeous or hypogeus, the surfaces tomentose, squamose or naked, erect stems represented by the inflorescence peduncles or absent. Leaves reduced to scales present only on the peduncles of the spadices in imbricate spirals, transformed into hexagonal peltate scales which form a crustose covering of the spadix and fall before anthesis, or reduced to an annulus of leathery laciniate tissue. Inflorescences spadix-like, short to long-pedunculate, flowering portion globose to cylindrical or clavate. Flowers small and densely crowded on the surface of the spadix (capitulum) or intermixed with a dense mat of filiform paraphyses (hairs), unisexual or bisexual. Flowers small and radially symmetrical, unisexual, male flowers naked or with a 3- to 8-lobed valvate perianth, stamens generally equal in number to the perianth lobes and opposite them, filaments free or connate to form a tubular column, anthers free or united, usually 2-theous, attached by their basal or dorsal surface, dehiscing by a lateral longitudinal slit or by an anterior-apical fissurate pore. Female flowers lacking a perianth or the perianth reduced and adnate to the ovary, the free limb small, truncate, 2-lobed or tubular, ovary globose-ellipsoid to prismatic-obovoid, 1- to 3-locular, styles terminal, 1 or 2, filiform and elongate or short and subclavate, the stigmas simple and discoid to capitate. Fruit small 1-seeded achenes or slightly fleshy and drupelike; seeds globose or compressed, testa thin or lacking, endosperm rich in fatty substances.

A family of about 18 genera and twice as many species in urgent need of more intensive study. The relationship of the Balanophoraceae to other families of the Santalalean alliance is at best obscure and likely to prove unnatural. The alliance

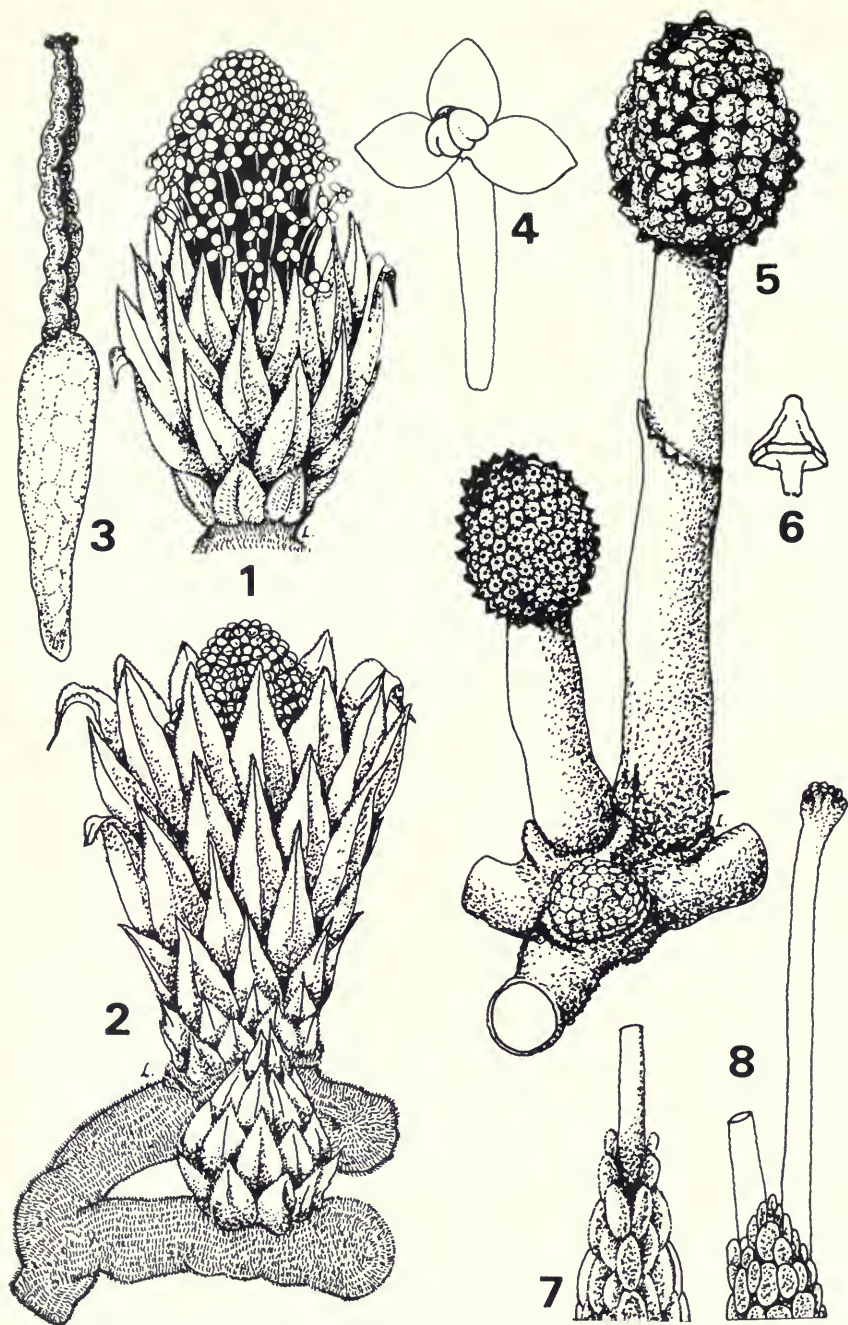


FIG. 15. Balanophoraceae. 1–4, *Langsdorffia hypogaea*: 1 & 2, inflorescences; 3, female flower; 4, male flower. 5–9, *Helosis cayennensis*: 5, inflorescence; 6, peltate scale; 7, female flower, lateral view; 8, female flower, frontal view; 9, male flower. 10–14, *Corynaea crassa*: 10, inflorescence; 11, male flower; 12, peltate scale; 13, paraphysate trichomes, uniseriate and crotaliform apices; 14, female flowers. 15 & 16, *Corynaea sphaerica*: 15, inflorescence; 16, peltate scale. Refer to Figure 16 also.



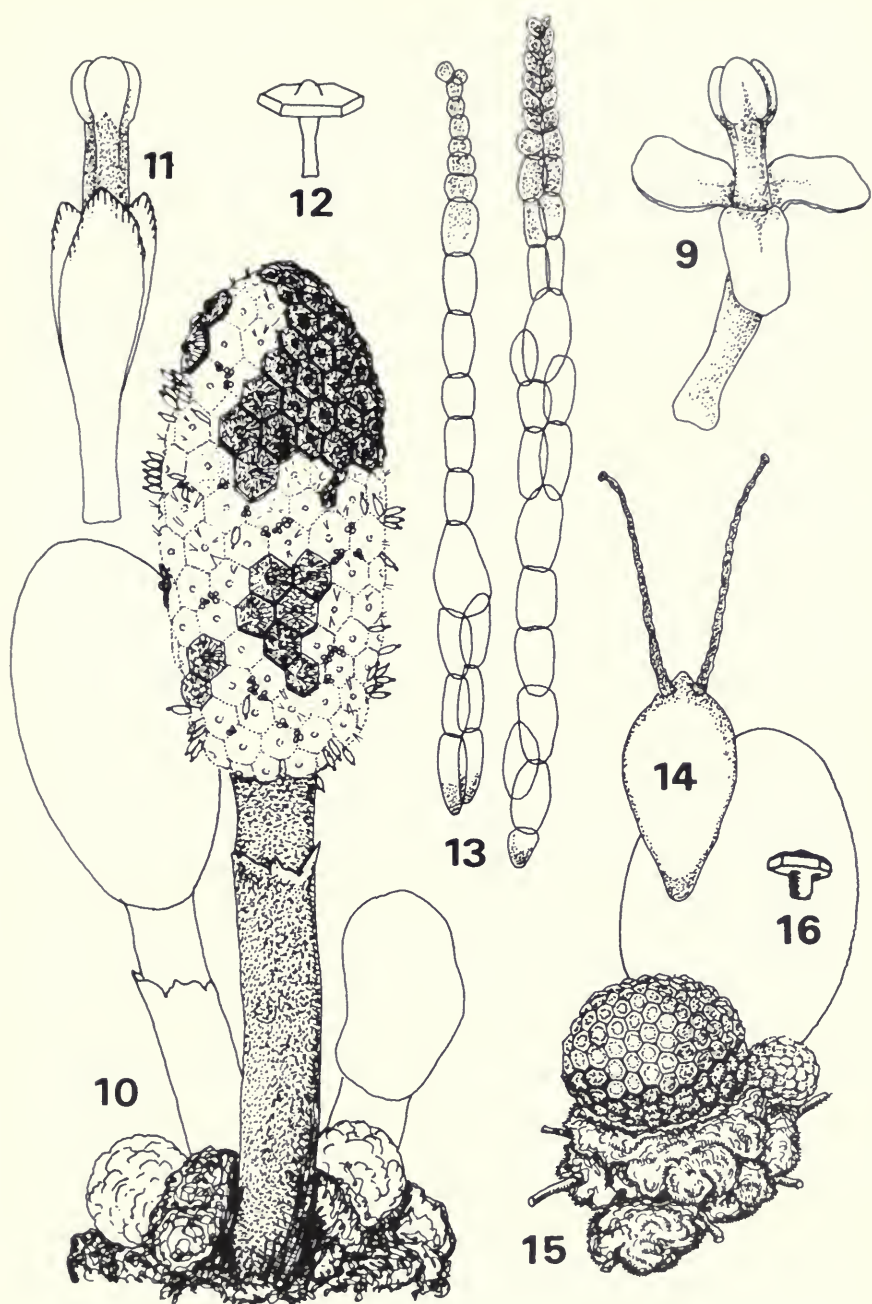


FIG. 16. Balanophoraceae: see Figure 15 for explanation.



of this family may be with the Gunneraceae. These unusual parasitic plants are represented by three genera and perhaps four species in Costa Rica.

- 1a Peduncle of the inflorescence ensheathed by many stiff imbricate, lanceolate scales to 3 cm long; rhizome elongate and branched, tomentose or velutinous; flowers not imbedded in a mat of filiform hairs; style 1.....*Langsdorffia*
- 1b Peduncle of the inflorescence not covered by large imbricate scales, peduncle of variable length or the inflorescence almost sessile, always covered by a crustose layer of small peltate scales caducous at anthesis; flowers imbedded in a dense mat of filiform hairs (paraphyses); styles 2.....2a
- 2a Perianth of male flowers with 3-6 tepals, connate in the lower half to form a tube and with the lobes always reflexed; stamens free at the apex but connate in the lower half (the apex often held together as a unit by an adhesive mucus of the anthers), anthers with 3 pollen sacs, 1 anterior and 2 posterior.....*Helosis*
- 2b Perianth of male flowers completely connate or the parts free in the upper half, the perianth lobes never reflexed but the margins always somewhat crenate; stamens connate in their entire length to form a tube, anthers with 2 lateral pollen sacs.....*Corynaea*

### CORYNAEA Hooker f.

Herbaceous root parasites, rhizomes nodular, globose or very rarely elongate, varying in size from a few centimeters to 35-40 cm in diameter. Inflorescence usually monoecious and proterogynous, rarely dioecious, peduncle emerging from an annular basal volva which disintegrates quickly, glabrous except for occasional annular appendages, capitulum or spadix globose to cylindrical or claviform, before anthesis covered by a compact layer of 6-sided, peltate and umbonate scales under which a substrate of dense filiform paraphyses surround the flowers, distal peltate portion of the scales caducous at anthesis, the pedicels of the scales forming areolae with male flowers along edges and corners of the areolae and female flowers within the areolae around the pedicels of the hexagonal (but deciduous) scales. Male flowers with a tubular or subcampanulate perianth, entirely connate or free in the upper half, perianth lobes 3, always crenate and never reflexed; stamens 3, exserted, filaments united into a column, anthers each with 2 lateral pollen sacs and forming a synandrium of 6 thecae; pollen 3- (5-) colpate, globose; some male flowers have a much-reduced pistillode. Female flowers without an apparent perianth or the perianth adnate to the pistil and reduced to a low epigynous collar with 2 inconspicuous segments; pistil 2-carpellate, ovary compressed, ovules 2, of which only 1 matures, styles 2, filiform and divergent, deciduous, stigmas slightly capitate. Fruit a 1-seeded achene with a hard epicarp and endocarp.

A genus of yellowish brown to deep purple root parasites that have not been found below 1,000 m elevation. Hansen (1980) considers the genus to be composed of a single species, *Corynaea crassa*, but Costa Rican material does appear to fall into two species.

- 1a Inflorescences pinkish in color, capitulum globose to ellipsoid or fusiform in shape.....*C. crassa*
- 1b Inflorescences golden yellowish brown in color, capitulum spherical to globose-elongate in shape.....*C. sphaerica*

***Corynaea crassa* Hooker f., Trans. Linn. Soc. London 22:31. t. 13. 1856. Figure 16.**

Inflorescence pink by the concentration of pigments in the glandular apices of the paraphysate trichomes which are 1.5-2.4 mm long, uni- or pluriseriate in which case the apex is crotaliform. Capitulum globose to elliptical or fusiform, up to 12 cm long and 4 cm in diameter, when immature covered by scales 3-4 mm in diameter, peltate on a pedicel 3-4 mm long. Staminate flowers up to 5 mm long with a 3-lobed perianth, the lobes 3-3.5 mm long and 1-1.4 mm wide, free in the upper  $\frac{2}{3}$  below which they form a tight tube of wide base; stamens 3, connate into a thick and long staminal column, anthers clavate and massive; pistillodes absent; pistillate flowers lacking a perianth, ovary obovoid, styles 2,

divergent, filiform and tapering at the apex, stigmas subdiscoïd-capitate. Fruit obovoid, large (up to 1.5 mm long).

Parasitic on *Quercus*, *Chusquea*, and *Vitis* in the mixed forest at high elevations. The inflorescences are visited by many flies and occasionally by *Bombus* bees; the fruit are scattered by staphylinid beetles which forage on the paraphysate trichomes and also rear their larvae in the outer layers of the rhizome which is of a bright cadmium yellow when freshly cut and rapidly oxidizes into a rusty brown. Although the rhizomes are often exposed and seem fleshy enough to attract herbivores, they contain a bitter principle that probably detracts predation.

***Corynaea sphaerica* Hooker f., loc. cit. t. 14. Figure 16.**

Rhizome tuberous, irregularly lobate, often velutinous and not more than 10 cm in diameter. Inflorescences bisexual, solitary or rarely 2 per rhizome, peduncles very short (less than 1 cm) or almost lacking, emerging from a persistent and thick annular volva, capitulum spherical or globose-elongate, up to 6 cm in diameter, when immature covered by spirally arranged rows of shortly peltate, wide scales, paraphysate trichomes abundant and dense, golden brown, up to 1.5 mm long, mostly uniseriate. Staminate flowers sub-immersed, with an obscure perianth of 3 connate lobes forming a campanulate infundibulum, stamens 3, fused into a tube 2.5 × as long as the width of the perigonial funnel, anthers and pollen like those of *C. crassa*; laterally compressed pistillodes sometimes present. Pistillate flowers lacking a perianth, styles 2, rather short and parallel, stigma discoïd, ovules 1. Fruit not seen.

Parasitic on *Chusquea* and *Euterpe* (?) in the high elevations of Talamanca. It differs little from the preceding species, the most important character being the mixed distribution of male and female flowers and the golden brown color of the paraphysate trichomes.

**HELOSIS Richard**

Herbaceous root parasites, rhizomes fleshy, tuberous, emitting elongate hypogean branches from which emerge the erect peduncles (flowering stems or spadices). Inflorescences borne on short or long peduncles that are annulate at the base or higher, capitulum broadly ovoid or globose, at first covered with hexagonal peltate valvate scales but these deciduous before anthesis, the inflorescences bisexual, the mixed male and female flowers in mammillate areoles and subimmersed in a dense mat of slender clavate paraphysate trichomes. Male flowers with a cylindrical perianth united near the base and with 3 ovate, concave, valvate and strongly reflexed distal lobes; stamens 3, filaments connate to form a tube up to 7 mm long, often with the filaments free in the upper third and directed outward or the anthers remain joined and the filaments become arcuate beneath them, anthers 3, basifixed and united into a 9-thecous synangium (each anther 3-thecous and cordate); pollen 3-colpate, ca. 30  $\mu$ m in diameter. Female flowers with superior perianth united to form a tube near the base and 2-labiate distally with 2 deltoid obtuse lobes; ovary ellipsoid, 1-locular, styles 2, long and filiform, stigmas capitate. Fruit a small 1-seeded achene with hard pericarp and oily endosperm.

*Helosis* includes only a single species, ranging from central Mexico through Central America and northern South America to Brazil and Bolivia. The plants range from sea level to 2,000 m elevation.

***Helosis cayennensis* (Sw.) Sprengel, Syst. Veg. 3:765. 1826. *Cynomorium cayennense* Swartz, Nov. Gen. & Sp. 12. 1788. *H. guyanensis* Richard, Mém. Mus. Hist. Nat. 8:416, t. 20. 1822, nom. illeg. superfl. *Caldasia cayennensis* (Sw.) Mutis ex Steudel, Nom. ed. 2. 1:255. 1840. *H. mexicana* Liebm., Förh. Skand. Naturf. 4, Möte 1844:181. 1847. *H. cayennensis* var. *mexicana* (Liebm.) B. Hansen, Svensk Bot. Tidskr. 72:188. 1978. Figures 15 and 16.**

Plants whitish, light brown or ferrugineous, glabrous, arising from a coralline tuberous rhizome. Peduncles solitary or clustered, erect, up to 10 cm long and 1 cm thick, with or without an annular process near the base or higher, capitulum ovoid or ellipsoidal-globose up to 6 cm long and 3 cm in diameter, before anthesis covered by peltate (stalk 2 mm) umbonate scales 3 mm in diameter which correspond to mammilate areoles densely covered by paraphysate claviform trichomes 1–2.5 mm long and densely pigmented. Perianth of staminate flowers a tube 2–3 mm long, 3-lobed, lobes ovate, 1–3 mm long, 0.5–1 mm wide; stamens 3, filaments connate, free at the apex when mature, anthers forming a syndrium 0.5–1 mm long, 0.5–1 mm in diameter. Pistillate flowers with a 2-labiate, fimbriate perianth, styles 2, 1.5 mm long, caducous, stigmas capitate. Fruit up to 2.25 mm long, ca. 0.5 mm broad.

Plants parasitic on the roots of a number of woody plants, found from the lowlands to elevations up to 1,600 m, in Costa Rica. The plant resembles a fungus, and like the species of *Corynaea*, it is called "hongo" by the local residents. Two other species have been described under *Helosis*, but I cannot find consistent differences to warrant their segregation. In Standley's *Flora of Costa Rica* (1937) and in Woodson & Schery's *Flora of Panama* (1960), this plant is cited or described as *H. mexicana* Liebm., the apparent confusion stemming from the peculiar behavior of the staminal tube which may be of connate filaments throughout its entire length, have the apices free or the anthers held together, while the immediate portion of the filaments are free and curved outward like a lantern (cf. Howard, *Rhodora* 61:79–81, 1959; Hansen, 1980).

*Helosis cayennensis* has been divided into two varieties by Bertel Hansen (1980); both of these varieties have been found in Costa Rica. The following key distinguishes them:

- 1a Peduncle with an involucre of 2–6 minute triangular scales near the base, the length of the peduncle divided by the length of the involucre (or annulus) to the base giving a value greater than 2.8; plants usually found below 1,000 m. . . . . var. *cayennensis*
- 1b Peduncle with the involucre represented by a more or less oblique, slightly swollen, ringlike mark (annulus) near the middle, the length of the peduncle giving a value of less than 2.8 when divided by the length of the ringlike involucre to the base; plants usually found above 1,000 m. . . . . var. *mexicana*

#### LANGSDORFFIA Martius, in Eschwege

Herbaceous fleshy root parasites with creeping or upright rhizome-like tubers dichotomously branched and tomentose-velutinous or glabrescent, stems (peduncles) bearing the inflorescences unbranched, surrounded at the base by a short toothed sheath (volva), covered by many imbricate stiff scales (scaly leaves). Leaves represented by the imbricate scales, ovate near the base and becoming progressively more lanceolate toward the apex surrounding the inflorescence. Inflorescences unisexual (rarely bisexual and monoecious) the flowering capitulum globose, to ellipsoid, capitate-clavate or ovoid, the male inflorescence taller than the female, the female often discoid or hemispherical. Male flowers pedicellate, with a perianth of 3 (rarely 2) concave, valvate tepals; stamens as many as there are tepals and opposite them, exserted, with short filaments connate into a column; anthers united into a syndrium with 6 pollen sacs, 4 at the base and 2 near the apex. Female flowers tightly congested, linear-prismatic, the perianth reduced to an obscurely 2- to 4-lobed collar, pistil solitary and the locule not apparent, ovule 1 and fused to the ovary wall, style 1 and caducous, stigma papillate. Fruit a small 1-seeded achene or drupaceous with a fleshy epicarp and hard endocarp.

A genus of yellowish or reddish root parasites resembling *Thonningia*, with one neotropical species ranging from southern Mexico to Brazil and Bolivia and a second, recently described, species from New Guinea. The stiff scaly covering of the flowering stems (inflorescences) readily distinguishes this genus.

**Langsdorffia hypogaea** Martius, in Eschwege, J. Brasil. 2:179, t. 5. 1818. Figure 15.

Herbaceous and thick-stemmed root parasites with the characters of the genus. Male inflorescences with peduncles (stems) up to 7 cm long, entirely covered by scales, the larger scales lanceolate, 4 cm long and 1 cm broad, the basal ones smaller and sparsely ciliate and stiff, capitulum ellipsoidal, 7–8 cm long and up to 4 cm in diameter; staminate flowers on long (10 mm) pedicels, petals 3, connate at the base to form a tube, free above with reflexed lobes, glabrous, petals 3–4 mm long and 1.5–2 mm wide; stamens 3 with filaments entirely connate, anthers subglobose-cordate dehiscent by slits, pollen 4-colpate, globose, smooth. Pistillate inflorescence of smaller dimensions, the capitulum or head discoidal to subglobose; female flowers with a short 2-lobed perianth 1.0–1.5 mm long and up to 0.5 mm in diameter, closely appressed to the style, the style up to 1.5 mm long, spirally twisted and laterally compressed, stigma subcapitate and minutely papillate.

Parasitic on the roots of *Ficus*, *Sapium*, and *Palmae* in elevations above 1,500 m in the Cordillera Volcanica Central. The pistillate flowers form a mat of coalescent structures due to a resinous or waxy secretion which burns easily.

### POLYGONACEAE

Herbs, shrubs, trees, or climbers, terrestrial or semiaquatic, bisexual or unisexual, glabrous or puberulent, stems often with thickened nodes, internodes solid or hollow; stipules forming a sheathing tube (the ocrea or ochrea) that surrounds the stem, usually deciduous and leaving a scar encircling the stem (absent in *Eriogonum* of N. America). Leaves alternate and simple, in a spiral or distichous (absent in *Muehlenbeckia platyclada*), petiolate, laminae entire or pinnately lobed, usually pinnately veined. Inflorescences usually an unbranched axis with alternating fascicles of flowers, less often with the flowers solitary, axillary, or cymose, the axes racemose or spikelike but occasionally borne on a leafless terminal twig and forming a compound paniculate arrangement, the flower fascicles usually subtended by a sheathing (ocreate) bract and the flowers subtended by thin translucent (ocreolate) bracteoles. Flowers usually radially symmetrical, bisexual or functionally unisexual, usually small, often borne on articulated pedicels, the perianth 3- to 6-parted, in 1 or 2 whorls of 2, 3, or 5 parts, the inner and outer whorls often not clearly differentiated (tepals), the outer parts often persistent or enlarging in fruit; stamens (4) 6–9, often in 2 whorls, filaments free or united at the base, borne on the base of the perianth or on the edge of a short hypanthium, anthers 2- or 4-thecous, often versatile and introrse; gynoecium of a solitary pistil with 1 locule and 1 basal orthotropous ovule, ovary superior and often 3-angled or lenticular, stigmas and carpels usually 3 (2–4). Fruit an achene with usually smooth hard surface, often tightly enclosed within the persistent and expanded outer perianth, the perianth sometimes forming wings, hooks, or tubercles as aids to dispersal; seed with a straight or curved embryo and mealy endosperm.

A cosmopolitan family of about 40 genera and 800 species, well represented in the north temperate zone as well as the tropics and subtropics. The unusual stipular tube leaving an encircling scar around the often thickened node is a distinctive vegetative feature. Some Commelinaceae have similar leaf bases, but the leaves are never pinnately veined. The small (less than 1 cm) flowers, often borne on spikelike axes and subtended by thin scarious bracteoles, are also distinctive.

#### KEY TO THE GENERA OF POLYGONACEAE IN COSTA RICA

- 1a Climbing plants with tendrils borne at the ends of inflorescences or leafless shrubs with flat ribbonlike stems; usually found in gardens but occasionally escaped; the stipules reduced to a thickened line around the stem at the nodes ..... 2a
- 1b Plants with leaves and without tendrils; the stipules usually forming a tube (ocrea) around the shoot apex, the ocrea persisting or deciduous and leaving a line around the stem. .... 3a



- 2a Climbing plants with tendrils terminating the inflorescence; laminae cordate to triangular; plants often growing along fences in gardens, with bright pink (or white) sepals ..... *Antigonon*
- 2b Shrubs or very short many-branched trees, the distal green stems 1–3 mm thick and 1–2 cm broad with transverse lines ..... *Muehlenbeckia platyclada*
- 3a Plants herbaceous, stems not woody except sometimes near the base; flowers bisexual or less often unisexual. .... 4a
- 3b Plants with woody stems, trees, shrubs, or climbers; flowers unisexual or bisexual. .... 6a
- 4a Leaves with palmate venation; plants grown in gardens for food ..... *Rheum*
- 4b Venation pinnate; plants not cultivated for food ..... 5a
- 5a Perianth of 2 whorls of 3 parts, the inner 3 expanding in fruit and often with grainlike tubercles, the flowers often in verticels, filaments shorter than the anthers, stigmas fimbriate; leaves often dimorphic with broader basal leaves. .... *Rumex*
- 5b Perianth of 3–5 subequal parts, not expanding in fruit; filaments longer than the anthers, stigmas capitate; leaves rarely dimorphic (in ours); plants often found in wet sites ..... *Polygonum*
- 6a Achenes enclosed but not greatly exceeded by a dry or succulent perianth, the fruiting perianth without long distal wings, perianth usually 5-parted; trees, shrubs or climbers, without spines ..... 7a
- 6b Achenes enclosed and exceeded by a thin, dry, expanded perianth, the fruiting perianth with 3 conspicuous long thin distal wings; perianth 6- (rarely 3-) parted; trees or spine-bearing shrubs. .... 9a
- 7a Trees or large erect shrubs, often with thick stems, not growing wild above 1,000 m in our area; inflorescences with thick (more than 3 mm) axes, flowers functionally unisexual and with a cuplike hypanthium ..... *Coccoloba*
- 7b Climbers and scrambling shrubs, growing wild or cultivated above 1,000 m elevation in our area; inflorescences with slender axes ..... 8a
- 8a Native plants found only above 1,400 m elevation; laminae cordulate and with more than 6 pairs of secondary veins; flowers unisexual, pedicels articulated beneath the flowers and lacking wings. .... *Muehlenbeckia*
- 8b Cultivated or escaped plants only known from around 1,100 m elevation; laminae cordate and with 3–5 pairs of secondary veins; flowers bisexual, pedicels with wings and articulated at the base ..... *Bilderdykia*
- 9a Fruiting perianth with the wings expanded from the back of the midrib and decurrent on the pedicel; stems with solid internodes and short terminal spines and with small (3 mm) rounded short shoots from which leaves and flowers arise in fascicles; laminae less than 8 cm long and with fewer than 7 pairs of secondary veins ..... *Podopterus*
- 9b Fruiting perianth with the wings expanded distally and long-spatulate or oblanceolate; stems lacking spines, flowers in racemose or paniculate arrangements ..... 10a
- 10a Internodes hollow and often with biting ants; leaves with more than 12 pairs of major secondary veins, 15–35 cm long; achene with 3 sharp ridges and 3 flat or concave faces, tightly enclosed within the fruiting perianth ..... *Triplaris*
- 10b Internodes solid; leaves with fewer than 12 pairs of major secondary veins, 3–18 cm long; schene with 3 deep longitudinal sulci separating 3 rounded sides, loosely enclosed within the fruiting perianth ..... *Ruprechtia*

### ANTIGONON Endlicher

Climbing plants with tendrils borne on the ends of the inflorescences, bisexual, glabrous or more often puberulent, stems thin and herbaceous or slightly woody; stipules reduced and leaving a small (often obscure) thickened line around the stem. Leaves alternate in a spiral, petiolate, laminae cordate to deltoid or sagitate, acute to acuminate at the apex and often with the midvein extended to form a small (1–3 mm) mucronate tip. Inflorescences basically a single racemose axis with alternating clusters of flowers, solitary and axillary but occasionally terminal and forming paniculate arrangements by the failure of subtending leaves to develop, the flower-fascicles subtended by small floral bracts. Flowers bisexual, borne on articulated pedicels, perianth of 5 parts with the outer 3 usually broader

than the inner 2, persisting and enlarging in fruit, stamens 8, free from the perianth, the filaments united to form a short tube, anthers 4-locular, ovary trigonous, styles 3 with 3 peltate stigmas. Fruit enclosed within the persisting and enlarged perianth parts, achene strongly 3-ridged in the upper (distal) part, surface smooth.

A genus of several poorly defined species, apparently native to Mexico and northern Central America. The plants are now widely cultivated because of the attractive inflorescences with long-persisting rose red or white perianth parts. The climbing habit, tendril-bearing inflorescences, and colorful stiff dry persisting perianth parts immediately distinguish this genus. These plants resemble the genus *Bougainvillea* in a superficial way. Collections of *Antigonon* from Costa Rica are few; the species have become naturalized only rarely.

- 1a Laminae not decurrent on the petiole and not forming conspicuous lateral wings on the upper part of the petiole; plants recorded from Costa Rica ..... 2a
- 1b Laminae decurrent on the petiole and forming conspicuous lateral wings (or margins) on the petiole; floral bracts small (less than 4 mm) and inconspicuous; plants not included in the descriptions ..... 3a
  - 2a Petioles short (less than 10 mm) and often obscured by the broad basal lobes of the lamina; floral bracts ca. 5 mm long and ovate; outer perianth parts becoming 3.5 cm long in fruit, with rounded apex and overlapping cordate basal lobes ..... *A. guatemalense*
  - 2b Petioles to 30 mm long and usually easily seen within the broad sinus of the lamina lobes (in pressed material); floral bracts 1–3 mm long, lanceolate; outer perianth parts rarely more than 1.5 cm long in fruit, acute at the apex and subcordate at the base ..... *A. leptopus*
- 3a Perianth reddish in color, outer perianth parts becoming 2 cm long in fruit, broadly rounded in outline; staminal tube very short ..... (?) *A. cinarascens* Mart. & Gal.
- 3b Perianth whitish or yellowish, outer perianth parts becoming 1.3 cm long in fruit, acute at the apex; staminal tube half the length of the pistil .. (?) *A. flavescens* Wats.

***Antigonon guatemalense*** Meisn., in DC., Prodr. 14:184. 1856. *Polygonum grandiflorum* Bertol., Fl. Guat. 412. 1840, not *P. grandiflorum* Willd., 1799. *A. grandiflorum* (Bertol.) Robinson, Proc. Amer. Acad. 44:513. 1909. *A. macrocarpum* Britton & Small, Sci. Surv. Porto Rico and Virgin Isl. 5:266. 1924. Figure 19.

Climbers, usually in thickets and shrubs to 2 m high, leafy internodes 1.5–15 cm long, 0.5–4 mm thick, densely short (0.3 mm) brownish puberulent. Leaves with petioles 2–10 mm long, densely brownish tomentulose, often obscured by the lamina base; laminae 6–15 cm long, 3.5–10 cm broad, broadly ovate to ovate-triangular, tapering gradually to an acute apex, cordate to cordulate at the base with the basal sinus usually narrow and obscuring petiole and node, margin entire, laminae drying thin chartaceous, densely soft puberulent below, venation pinnate with 3–6 pairs of major secondary veins. Inflorescences solitary and axillary with a single axis but occasionally terminal with several axes in a panicle arrangement, to ca. 25 cm long, the alternating flower fascicles 5–25 mm distant on the rachis, subtended by conspicuous broadly ovate floral bracts, ca. 5 mm long and with a cuspidate apex, puberulent, pedicels 8–25 mm long, densely and minutely (0.2 mm) puberulent; flowers with the perianth parts ca. 4 mm long before anthesis, staminal tube relatively short and thick. Fruit enclosed within the persisting perianth, the outer perianth parts becoming 3.5 cm long, cordate at the base with the basal lobes usually overlapping, rounded to emarginate at the apex, venation prominent on the surface of the perianth, fruit narrowly ovoid, with 3 sharply defined longitudinal ridges on the upper half, ca. 10 × 5 mm, lustrous and pale brown or greenish.

Plants cultivated in gardens or found as escapes in secondary growth between (0) 200 and 1,500 m altitude. The species appears to be native in Guatemala and is now widely distributed in the tropics and subtropics.

*Antigonon guatemalense* is recognized by the usually cordate leaf bases obscuring the short petioles and nodes, the generally dense brownish puberulence, the



FIG. 17. Polygonaceae: species of *Polygonum* in Costa Rica.



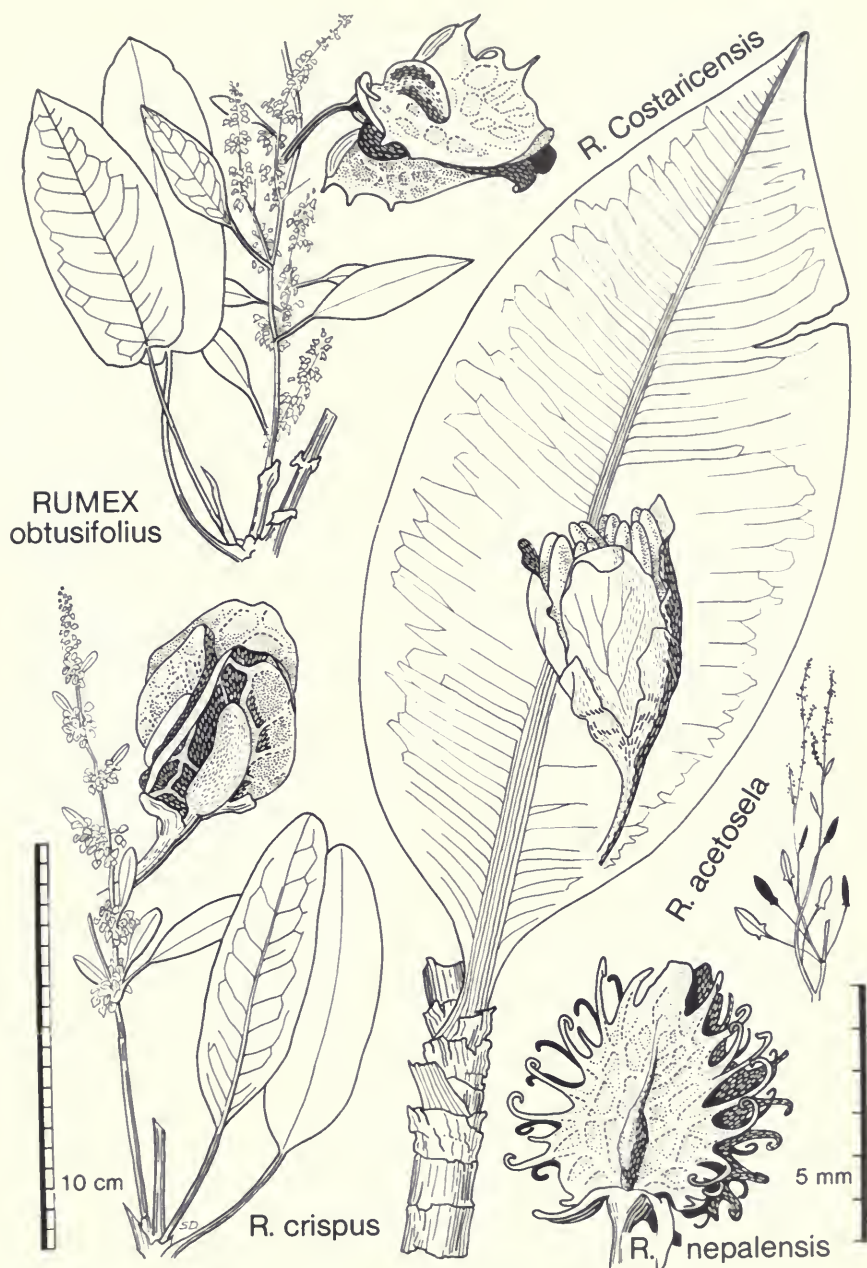


FIG. 18. Polygonaceae: species of *Rumex* in Costa Rica.



**MUEHLENBECKIA**  
**tamnifolia**

**ANTIGONON**  
**leptopus**



FIG. 19. Polygonaceae: wild and ornamental climbing plants in the genera *Antigonon*, *Bilderdykia*, and *Muehlenbeckia*.



FIG. 20. Polygonaceae: trees and shrubs with winged fruits; species of *Podopteris*, *Ruprechtia*, and *Triplaris*.

broad little floral bracts at the base of the flower clusters, and the large pink perianth parts enclosing the fruit. The common names *Bellísima*, *Colacion*, *Confite*, *Confitillo*, and *San Andres* have been used for these plants in Central America.

***Antigonon leptopus*** Hook. & Arn., Bot. Beechey Voy. 308, pl. 69. 1839–1840. *A. cordatum* Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles 10, pt. 1:14. 1843. Figure 19.

Climbers to over 10 m high but more often only 1 or 2 m high, leafy internodes 1–10 cm long, 1–4 mm thick, sparsely to densely puberulent. Leaves with petioles 4–30 mm long, 0.5–1.5 mm thick; laminae 3–15 cm long, 2–10 cm broad, broadly ovate to sagitate, acuminate to acute at the apex, subcordate to cordate at the base with a usually broad open sinus, margin entire or undulate, laminae drying thin chartaceous, sparsely to densely puberulent beneath with small (0.1–0.3 mm) brownish hairs, venation pinnate with 5–9 pairs of major secondary veins. Inflorescences solitary and axillary with a single axis but also terminal and forming a compound panicle, to 25 cm long, flower clusters 5–20 mm distant on the rachis, floral bracts 1–3 mm long, lanceolate, sparsely puberulent, the pedicels 2–10 mm long; flowers ca. 4 mm long when buds open for anthesis, staminal tube ca. half the length of the pistil. Fruit enclosed within the persistent and enlarged perianth parts, the perianth parts to 15 mm long and 12 mm broad (rarely? to  $25 \times 12$  mm), acute at the apex, subcordate at the base, very sparsely or very minutely (0.5 mm) puberulent, the venation raised on the abaxial surfaces when dry, body of the fruit ovoid, 3-angled with 3 longitudinal ridges near the apex, ca.  $9 \times 5$  mm, lustrous and pale brown.

Plants cultivated in gardens or occasionally escaped and climbing over low shrubs (especially along river banks), rarely found above 1,000 m altitude in Central America. The species is probably native to Mexico, but is now widely planted in warmer parts of the world.

*Antigonon leptopus* is recognized by the broadly cordate or subcordate leaf bases, the inconspicuous floral bracts, the persisting perianth parts which are pink to rose or deep rose red, and the usual association with gardens. This species is called *Bellísima*, *Confite*, *Flor de San Miguel*, and *San Miguel* in Central America.

#### BILDERDYKIA Dumort

Woody or herbaceous, climbing or decumbent, slender stemmed; ocreate stipules present and persisting. Leaves alternate in a spiral, petiolate, laminae deltate to cordate or sagittate, glabrous or very minutely puberulent. Inflorescences solitary, axillary or terminal, flowers usually in small fascicles subtended by ocreate bracts, on spikelike or raceme-like axes that may be part of a paniculate arrangement (as in ours); flowers bisexual and regular, borne on articulate pedicels, perianth composed of 5 parts united near the base, the 3 outer perianth parts with longitudinal keels or wings on the midrib abaxially, stamens 6–9 and borne on the edge of a shallow cup, filaments of 2 lengths, ovary superior and free of the cup, styles absent, stigma capitate. Fruit a 3-angled nut, usually included in and not exceeding the persisting perianth, perianth becoming pink and the nut black.

A small genus once included in *Polygonum* and native to Europe and Asia.

***Bilderdykia aubertii*** (Henry) Moldenke, Revista Sudamer. Bot. 6:29. 1939. *Polygonum aubertii* Louis Henry, Rev. Hort. 1907:82–83. 1907. *P. baldschuanicum* auct., non Regel. Figure 19.

Woody climbers to 5 m high, the distal stems thin and pendent, bisexual, leafy internodes 1–10 cm long, ca. 2 mm thick, glabrous, drying pale in color and with longitudinal ridges; ocreate stipules 2–3 mm long, thick, brown, the basal parts persisting. Leaves alternate, petioles 1–4 cm long, slender and glabrous, with 2 adaxial ridges forming a narrow sulcus; laminae 2–9 cm long, 1.5–5 cm broad, ovate to ovate-triangular in outline, tapering to an acuminate apex, cordate to subcordate at the base and decurrent on the

petiole, margin entire, drying chartaceous, smooth and essentially glabrous on both surfaces, venation pinnate or subpalmate with 3–5 pairs of major secondary veins. Inflorescences solitary and axillary or terminal, to 15 cm long, paniculate with alternate racemose branches, flower-bearing rachis slender and with minutely papillate-puberulent longitudinal ridges, pedicels ca. 2 mm long, articulate near the base and with 3 wings enlarged distally; flowers bisexual, ca. 1.5 mm long (open) and 3 mm broad, the 3 outer perianth parts with conspicuous wings that are continuous with the wings of the pedicel, inner perianth parts smaller, stamens mostly 8 or 9, ovary strongly 3-angled and with large papillate stigmas. Fruit not seen.

A trailing climber in shrubs about 2.5 m high and apparently growing wild in the city of San Jose at 1,100 m elevation; flowering in September. We have no other record of this genus and species in Central America.

*Bilderdykia aubertii* is recognized by the glabrous cordate leaves on thin hanging stems, the small white flowers in open paniculate inflorescences, and the thin wings on the back of the outer perianth parts decurrent on the pedicel. This species is planted in Europe as an ornamental climber; it is native to western China and Tibet. This species also is referred to as *Fallopia aubertii* (Louis Henry) J. Holub or as *Polygonum aubertii* Louis Henry. English names are "Silver Lace Vine" and "China Fleece Vine."

#### COCOLOBA Patrick Browne ex Linnaeus

REFERENCES: R. A. Howard, Studies in the genus *Coccoloba*, VII. A synopsis and key to the species in Mexico and Central America. J. Arnold Arbor. 40:176–220. 1959. R. A. Howard, in R. E. Woodson, Jr., and R. W. Schery, *Coccoloba* in the Flora of Panama. Ann. Missouri Bot. Gard. 47:340–353. 1960.

Shrubs or trees, rarely scramblers or lianas (none in Central America), usually unisexual, leafy stems usually thick and terete, glabrous to puberulent or with glandular excretions resembling small trichomes, often longitudinally striate, the pith solid or the internodes sometimes hollow, the nodes usually thicker than the internodes; stipules united to form a tube (the ocrea) around the stem, the ocrea initially enclosing and protecting the shoot apex and then splitting as the apex develops, the distal sheathing part of the stipule usually thin and deciduous, the basal part usually thicker and often persisting, occasionally extending below the petiole base, glabrous to puberulent, leaving a scar around the stem. Leaves alternate and simple, persistent or deciduous, often varying considerably in size on the same plant, the leaves of juveniles and adventitious shoots often much larger than leaves on distal branches; petiole borne at the base or above the base of the differentiated stipule enclosing the node, usually canaliculate or sulcate (grooved) above (ad-axially); laminae entire or undulate, venation usually pinnate, often quite stiff, glabrous to puberulent or with glandular excretions. Inflorescences terminal or terminal on short lateral shoots, unisexual, basically a single unbranched axis but occasionally branched near the base or the axes in a paniculate arrangement on a short leafless terminal shoot, the peduncle (flowerless base) usually very short and not differentiated from the rachis, the rachis usually minutely puberulent and with longitudinal ridges, flowers borne singly or in fascicles on thickened areas of the rachis, subtended usually by a stiff bract and 1 or more thin ocreolate bracteoles, pedicels shorter or longer than the subtending bracteoles, the female flowers usually solitary, the male flowers usually several together in a fascicle. Flowers functionally unisexual but with organs of both sexes, perianth and staminal bases forming a small or distinct cuplike hypanthium, perianth 5- (6-, 7-) parted, imbricate in bud, becoming reflexed in male flowers but usually remaining appressed to the ovary and succulent in fruit in the female, stamens usually 8, functional stamens of the male flowers exerted, filaments free above, staminodes of the female flower included, and pistillode of the male flowers remaining included, the functional pistil of female flowers with 3 exerted styles and expanded stigmatic surfaces, ovary trigonous. Fruit included within the expanded and usually fleshy or succulent hypanthium and/or perianth lobes (essentially a drupe with loosely enclosed achene); the achene usually trigonous, surface smooth and brownish in color, outer wall hard, seed with ruminate endosperm.



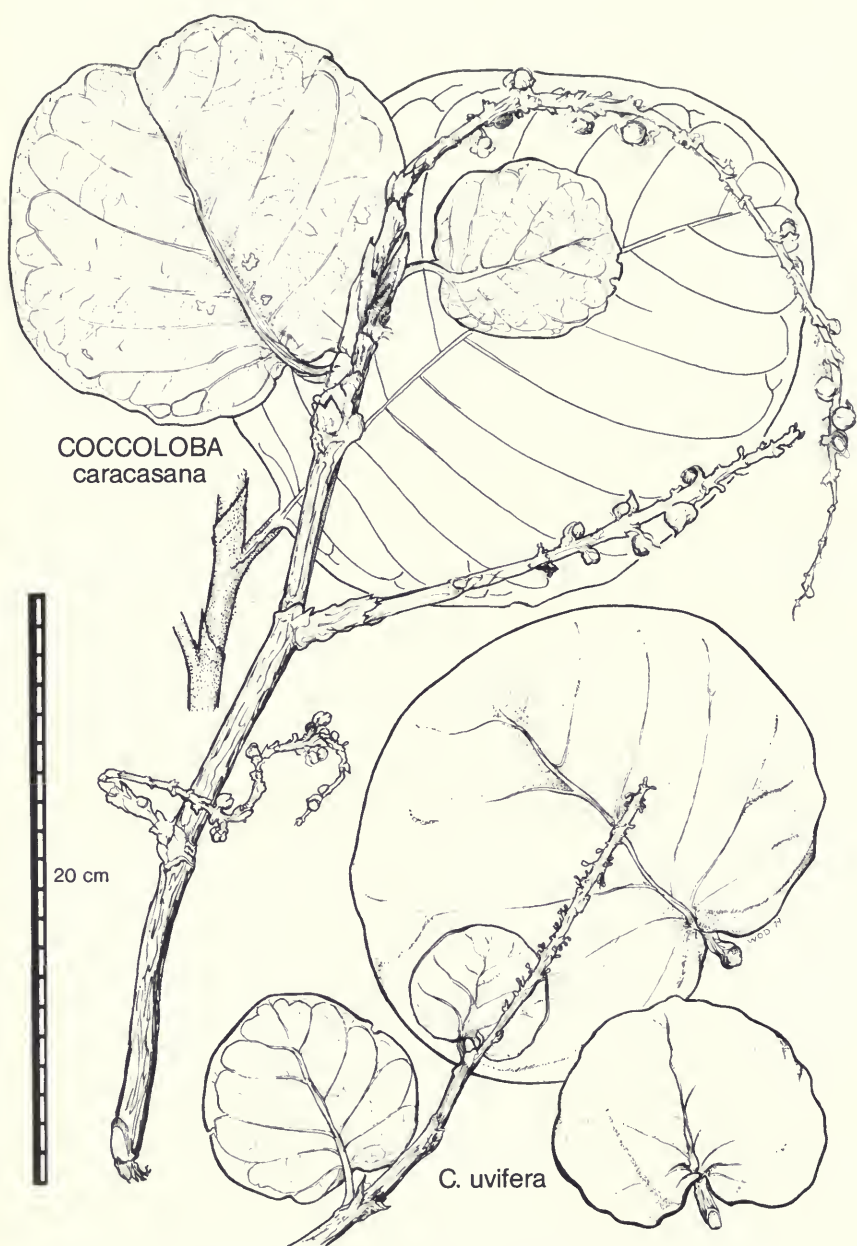


FIG. 21. Polygonaceae: two species of *Coccoloba* with larger rounded leaves.



FIG. 22. Polygonaceae: species of *Coccoloba* with petioles arising above the base of the associated tubular stipule.



FIG. 23. Polygonaceae: common species of *Coccoloba* with petioles arising near the base of the associated stipules.

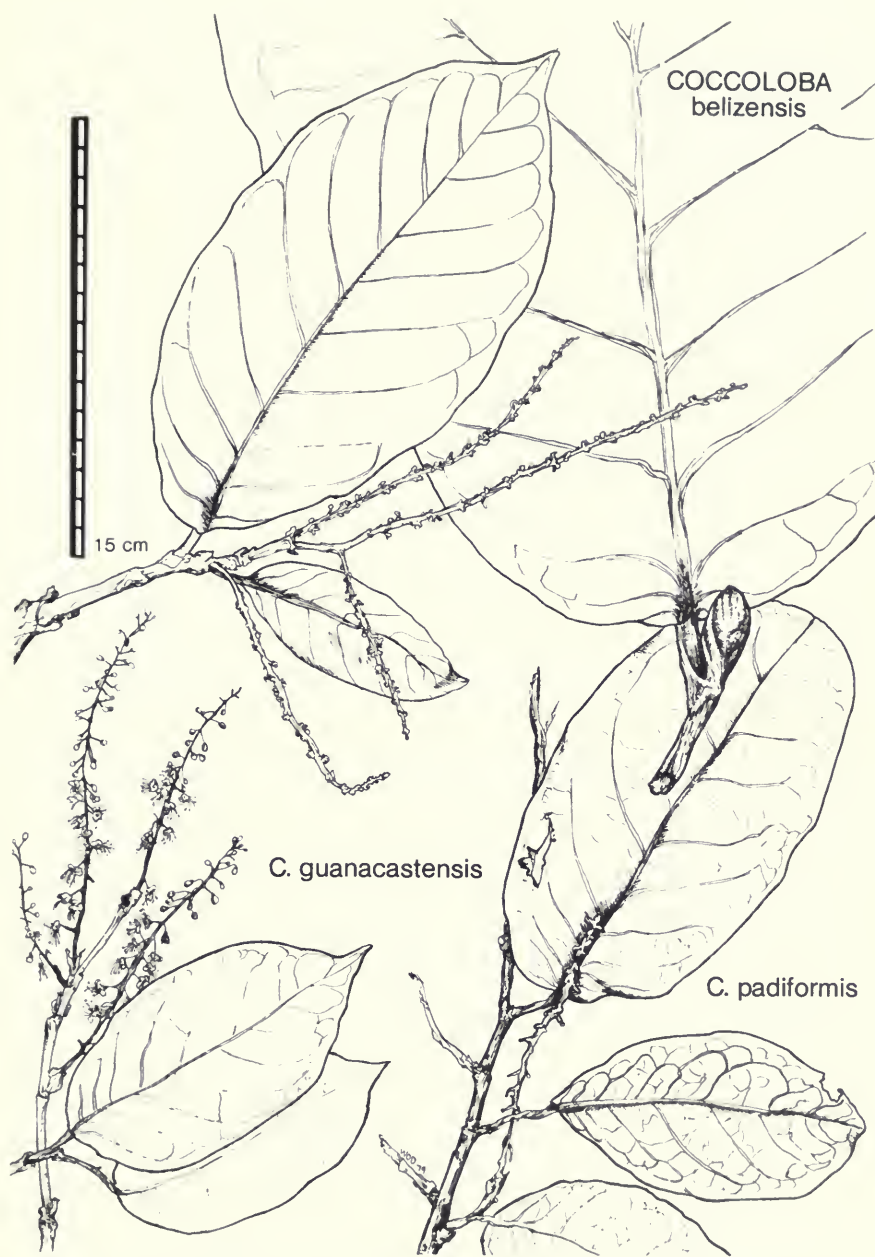


FIG. 24. Polygonaceae: rarely collected species of *Coccoloba* with petioles arising at or above the base of the associated stipules.



A genus of the American tropics with more than 100 species, best represented in the West Indies and South America. Our members of the genus can be recognized by the shrub or tree habit, ocreate stipules at first enclosing the shoot apex and leaving a scar around the stems, the usually thick twigs often with thickened nodes, usually stiff entire leaves with pinnate venation, small flowers subtended by thin tubular bracteoles and borne on a relatively thick and often unbranched axis, and a trigonous achene tightly enclosed within a thin succulent perianth. *Papaturro* is a commonly used name for members of the genus in Central America. None of our species grow above 1,000 m elevation in Costa Rica.

- 1a Petiole arising well above the base of the tubular stipule (ocrea), the diameter of the petiole scar smaller than the distance from the base of the petiole scar to the differentiated stipular base.....2a
- 1b Petiole arising at about the same level as the clearly differentiated base of the sheathing stipule.....6a
  - 2a Inflorescence panicle; distal internodes covered by the stiff persisting ocreae, leafy stems 6–15 mm thick, laminae usually over 18 cm long and 10 cm broad; wet evergreen forests below 1,000 m elevation ..... *C. tuerckheimii*
  - 2b Inflorescences usually solitary spikes or racemes; distal internodes usually visible between the ocreae, leafy stems to 7 mm thick, laminae generally not over 18 cm long; found mostly on the Pacific slope in Costa Rica.....3a
  - 3a Flowering and fruiting pedicels 2–15 mm long, the flowers clearly separate in early stages on a rachis only 1–2 mm thick; achenes not coronate at the apex.....4a
  - 3b Flowering and fruiting pedicels 1–4 mm long, the flowers densely congested in early stages, flowering rachis 2–3 mm thick; achenes coronate at the apex.....5a
    - 4a Laminae ovate to suborbicular, to 10 cm long, cordate to subcordate or peltate near the base, petioles 12–45 mm long, 0.6–1.5 mm thick; rare plants of the Pacific slope between ca. 500 and 1,000 m elevation  
*C. acapulcensis*
    - 4b Laminae oblong to obovate, to 20 cm long, sometimes rounded at the base but never cordate to peltate, petioles to ca. 25 mm long and 1–3 mm thick (dry), plants of dry deciduous lowland areas in Guanacaste  
*C. guanacastensis*
  - 5a Petioles 8–25 (60) mm long; fruit sessile or short (1–3 mm) pedicellate; laminae elliptic to obovate, abruptly narrowed at both apex and base (but never rhombic); evergreen or partly deciduous formations of the Pacific slope. *C. obovata*
  - 5b Petioles 8–11 mm long; fruit clearly pedicellate; laminae usually conspicuously and gradually narrowed to both apex and base, often rhombic in outline; low elevations around the Caribbean but not recorded from between Honduras and Central Panama and not included in the descriptions ..... *C. coronata*
- 6a Inflorescence panicle; terminal shoot at first enclosed in a spatulate or obovoid and bluntly rounded densely tomentulose ocreate stipule 1–4 cm long; laminae becoming 50 cm long and 25 cm broad on relatively short petioles; Caribbean lowlands ..... *C. belizensis*
- 6b Inflorescence a spike or raceme and these not in a panicle arrangement; shoot apex of terminal shoots not enclosed in a large spatulate covering .....7a
- 7a Laminae almost as broad as long to broader than long, stiffly subcoriaceous to coriaceous, rounded to emarginate at the apex.....8a
- 7b Laminae usually distinctly narrower than long, usually acute to acuminate at the apex (or rounded in *C. venosa*) .....9a
  - 8a Plants usually found near the sea shore but also planted for ornament; laminae usually broader than long and with 3–6 pairs of major secondary veins, coriaceous..... *C. uvifera*
  - 8b Plants of seasonally very dry areas along the Pacific slope below 500 m; laminae usually narrower than long and with 6–12 pairs of major secondary veins  
*C. caracasana*
- 9a Bracts and bracteoles subtending the flowers very small (less than 1 mm) and incon-

- spicuous, the flowers usually separate along the rachis and clearly pedicellate with the inflorescence racemose, both male and female flowers often solitary; plants glabrous and rare in collections. .... 10a
- 9b Bracts and bracteoles subtending the flowers usually more than 1 mm long, conspicuous and often obscuring the pedicels and the inflorescence appearing spicate (at least in early stages), puberulent, male flowers usually borne in groups of 2-5. .... 11a
- 10a Flowers 2-4 mm long; laminae with the tertiary venation obscure above when dry; trees of evergreen forests of the Pacific slope between sea level and 1,000 m. .... *C. padiformis*
- 10b Flowers 4-6 mm long; laminae with the tertiary venation forming a fine ( $\times 10$ ) reticulum on the upper surface (dry); plants of the deciduous lowlands of Guanacaste. .... *C. guanacastensis*
- 11a Laminae usually broadest above the middle, drying very stiffly chartaceous or subcoriaceous; inflorescences not usually exceeding 14 cm in length, the flowers usually closely crowded and the rachis not clearly visible; plants of the deciduous and partly deciduous formations of the Pacific slope below 300 m elevation. .... *C. venosa*
- 11b Laminae usually broadest at the middle (occasionally obovate in *C. lehmannii*), drying chartaceous to stiffly chartaceous; inflorescences usually exceeding 14 cm with the flowers or flower fascicles separate along the rachis. .... 12a
- 12a Inflorescence racemose, pedicels usually clearly visible, bracts usually perpendicular to the rachis; laminae broadly elliptic to elliptic-obovate, acute to short acuminate; wet evergreen formations, 0-1,000 m. .... *C. lehmannii*
- 12b Inflorescence spicate, pedicels usually hidden within the bracts, the bracts at an acute angle to the rachis; laminae narrowly elliptic and acuminate; evergreen or partly deciduous areas, below 300 m elevation. .... *C. acuminata*

***Coccoloba acapulcensis*** Standley, Proc. Biol. Soc. Wash. 33:66-67. 1920. *C. browniana* Standl., Trop. Woods 10:4. 1927. *C. wercklei* Standl., Publ. Field Columbian Mus., Bot. Ser. 4:304. 1929. *C. cardiophylla* Standl., Publ. Field Columbian Mus., Bot. Ser. 8:8. 1930. Figure 22.

Shrubs or small trees 2-6 (8) m tall, glabrous throughout, leafy internodes 0.5-8 cm long, 1-4 mm thick, smooth and glabrous, becoming striate, becoming dark brown and lenticellate; stipules 1-2 cm long, originating 7-12 mm below the base of the petiole, glabrous or very minutely puberulent, drying reddish brown and usually persisting, the apex of the ocrea often resembling a ligulate development on the leaf base. Leaves alternate in a spiral or distichous, often peltate in younger plants, petioles 10-45 mm long, 0.6-1.5 mm thick, smooth and drying brown, becoming articulate near the middle of the ocrea; laminae 4-14 cm long, 2.5-11 cm broad, ovate to suborbicular, rounded distally and very short-acuminate at the apex, rounded at the subcordate or peltate or truncate base, occasionally peltate with the petiole as much as 15 mm distant from the base of the laminae, margin entire or somewhat crenate-undulate, the edge becoming revolute, the laminae drying chartaceous pale brown or grayish, smooth and glabrous above and below, with 4-8 pairs of major secondary veins. Inflorescences terminal on axillary short shoots, 3-8 cm long, solitary and racemose, rachis 0.5-2 mm thick, glabrous, both male and female flowers solitary, bracts and bracteoles ca. 1 mm long; male flowers with filaments 2-3 mm long, anthers ca. 0.5 mm long; female flowers not seen. Fruit retained within the succulent perianth, about 2 cm long and 1.2 cm in diameter, globose or obovoid, perianth lobes only ca. 3 mm long at the apex of the fruit, fruiting pedicels 5-10 (15) mm long; achene difficult to remove from the perianth when dry, ca.  $16 \times 10$  mm, rounded-trigonus.

Plants of the seasonally dry Pacific slope and known in Costa Rica from only two collections: *Werckle s.n.* from near El Coyolar, and *Brenes 21872* from San Pedro de San Ramon, both from the province of Alajuela between 100 and 1,000 m on the Pacific slope. The species ranges from Guerrero and Yucatan in Mexico along the Pacific slope of Central America to central Costa Rica.

*Coccoloba acapulcensis* is recognized by its relatively small rounded (sometimes peltate) leaves on slender petioles articulated well above the stipular base, the lack

of pubescence on nearly all parts, small inflorescences with conspicuous pedicels, and relatively large fruit. The species is very poorly known in Costa Rica, and it may be restricted to the partly deciduous (tropical moist and premontane moist) forest formations between 100 and 1,000 m on the Pacific slope.

***Coccoloba acuminata*** H.B.K., Nov. Gen. 2:176. 1817. Figure 23.

Shrubs or small slender trees 1.5–5 (8) m tall, leafy internodes (0.2) 1–6 cm long, 1–3 (6) mm thick, glabrous or brownish puberulent, usually drying dark and smooth, sparsely lenticellate; stipules 3–15 mm long, the free distal portion of the tube truncate at the apex and caducous, densely brownish hirsutulous or (less often) very sparsely hirsutulous or with reddish brown glandular excretions. Leaves alternate and distichous, petioles 6–15 mm long, 0.8–1.5 mm thick, slightly sulcate above, hirsutulous or glabrous, arising from the base of the ocrea; laminae 7–16 (24) cm long, 2–6 (8) cm broad, narrowly elliptic to elliptic-oblong or lanceolate, gradually tapering to the long-acuminate apex, acute to obtuse at the base, margin entire, the laminae drying thin-chartaceous to stiff-chartaceous and often dark in color above, smooth and glabrous above or minutely papillate-puberulent on the midvein, glabrous below except for tufts of hairs in the axils of the major veins, often with small punctate glandular excrescences sparsely distributed over the lower surface, with 7–15 pairs of major secondary veins, the tertiary veins very thin and inconspicuous, the midvein raised above. Inflorescences terminal and solitary, 15–30 (45) cm long, the flower fascicles clearly separate along the slender (0.7–1.5 mm) rachis, peduncle 2–5 cm long, the rachis minutely (0.2–1 mm) puberulent to short-hirsute, thickened below each flower cluster, pedicels shorter than the subtending bracteoles; male flowers usually solitary, ca. 3 mm long, fertile pistil ca. 1 mm long with 2 or 3 styles. Fruit included within the succulent perianth, becoming globose and 6–8 mm in diameter (dry), the perianth parts united only near the base (at first) but the basal areas expanding and the lobes finally covering  $\frac{1}{2}$ – $\frac{2}{3}$  of the fruit, translucent white at maturity and drying black, pedicels 1–2 mm long and not exceeding the bracteoles; achene ca. 5–6 mm long and 4 mm broad, trigonous with rounded edges, broadest near the base, dark brown to tan, smooth and lustrous.

Plants of the lowland wet evergreen and partly deciduous forest formations below 300 m elevation; flowering and fruiting throughout the year, but collected most often in March and April. The species ranges from the Caribbean side of Guatemala, Honduras, and Nicaragua through Costa Rica and Panama to Peru and Brazil.

*Coccoloba acuminata* is recognized by the thin narrow acuminate leaves, long-pendulous spicate inflorescences with the flower groups clearly separate along the slender rachis, short pedicels hidden within the bracteoles (ocreolae) and the wet lowland habitat. The leaves resemble those of many tropical wet forest species, but differ strikingly from other members of the genus in our area. The species is known only from three collections in Costa Rica: *Allen 5226* from near the Río Terraba, Puntarenas, *Holm & Iltis 710* from the Río Frio, and *Standley 40189* from near the Río Grande de Tarcoles, both in the province of Alajuela. Recently, new records for Costa Rica have come from Santa Cruz, Guanacaste, near the Nicaraguan border. Despite the paucity of Costa Rican collections, the species appears to be common in southeastern Nicaragua and central Panama.

***Coccoloba belizensis*** Standley, Trop. Woods 16:38. 1928. *C. hirsuta* Standley, Publ. Field Columbian Mus., Bot. Ser. 4:303. 1929. Figure 24.

Small to large trees, reaching 30 m in height, leafy internodes 1–8 (12) cm long, 4–8 (14) mm thick, at first densely short (0.3 mm) hirsute but quickly becoming glabrous, (densely puberulent to tomentulose on adventitious and young shoots), the hairs yellowish brown to dark brown; stipules 1–4 cm long, forming an unusual spatulate cap over the shoot



apex, rounded at the apex and arising above the petiole base, densely brownish hirsutulous, splitting irregularly as the shoot expands. Leaves alternate, variable in size and often quite large, petioles 1.5–5 cm long, 3–8 mm thick, densely brownish hirsutulous with hairs 0.1–1 mm long, longitudinally striate and somewhat canaliculate above; laminae 16–30 (50) cm long, 8–14 (30) cm broad, oblong to broadly ovate, tapering to the usually bluntly obtuse apex, obtuse to rounded at the base and often cordulate at the petiole in larger leaves, margin entire and revolute on drying, subcoriaceous, quickly becoming glabrous and grayish-lustrous above, remaining minutely puberulent on the veins beneath (but remaining densely brownish hirsutulous in some), with 6–10 pairs of major secondary veins, the midvein raised within a depression above, tertiary veins obscure above but prominent and often subparallel beneath. Inflorescences to 20 cm long, panicle terminal arrangements of nearly equal racemose or spicate branches, flower fascicles separate on the minutely puberulent and deeply ridged rachis, pedicels not exceeding the bracteoles; male flowers several per fascicle, filaments ca. 1 mm long, anthers ca. 0.5 mm long; female flowers solitary. Fruit enclosed within the succulent perianth ca. 7 mm long and 6 mm in diameter, the perianth lobes free for about half the length of the fruit; achene ca. 5–6 mm long and 5 mm thick, ovoid to subglobose, weakly trigonous with rounded edges, surfaces lustrous brown.

Trees of the Caribbean lowlands below 800 m elevation; flowering and fruiting from May to October. The species, as presently known, ranges from Belize to eastern Nicaragua.

*Coccoloba belizensis* is easily recognized because of the unusual size and form of the ocreate stipules covering the shoot apices, the large leaves with relatively few secondary veins, and the panicle inflorescences. The leaves often dry with a very smooth, but not lustrous, upper surface that is pale gray or pale yellowish brown. While not yet recorded from Costa Rica or Panama, the species has been collected in eastern Nicaragua (Shank 93) and is said to be common along the Rio Grande in the Department of Yelaya (Molina 2509).

*Coccoloba standleyana* Allen, based on sterile material and described in *The Rain Forests of Golfo Dulce* (1956, pp. 177 & 409), probably belongs under *C. belizensis*, according to Howard (1959, p. 215).

***Coccoloba caracasana* Meisner, in DC., Prodr. 14:157. 1856. Figure 21.**

Small- to medium-sized trees 2–12 (20) m tall, often with multiple trunks and rounded crown, leafy internodes 0.5–6 (9) cm long, 2–6 (10) mm thick, minutely puberulent to hispidulous with brownish hairs 0.1–0.8 mm long, becoming glabrous and pale gray; stipules 10–20 (40) mm long, the distal tube membranaceous and deciduous, minutely (0.1–0.3 mm) puberulent or with resinous excretions. Leaves alternate and usually distichous, petioles 8–25 (40) mm long, 1.5–4 mm thick, inserted just above the thickened node on the base of the ocrea, densely reddish brown puberulent or glabrescent; laminae (5) 8–20 (37) cm long, (4) 6–15 (28) cm broad, broadly ovate to broadly oblong or suborbicular, rounded and often emarginate at the apex, rounded and truncate to subcordate at the base, margin entire and slightly undulate, the edge flat, the laminae drying stiffly chartaceous to subcoriaceous and dark brown or pale gray, smooth and glabrous above, minutely (0.1–0.5 mm) puberulent on the veins beneath or glabrous but with hairs in the axils of the major veins, with 6–10 (12) pairs of major secondary veins, the major and minor veins slightly raised on the upper surface when dry. Inflorescences terminal on short axillary shoots, 15–25 cm long, the rachis densely and minutely puberulent, 1.5–3 mm thick; male flowers 3–4 per fascicle and the fascicles often crowded on the rachis (but the rachis usually visible), filaments ca. 2 mm long, anthers ca. 0.4 mm long; female flowers solitary in the fascicles and the fascicles separate along the rachis, perianth lobes 1–1.5 mm long on a hypanthium 0.5 mm long. Fruit enclosed in the white semisucculent perianth, 4–6 mm long and ca. 5 mm in diameter when dry, the perianth lobes free almost to the base (covering  $\frac{2}{3}$  of the achene), the fruit borne on short (2–3 mm) pedicels; achenes 3–5 mm long, strongly 3-angled with 3 distinct longitudinal ridges, broadest near the base, becoming dark brown, smooth and lustrous.



Trees of the seasonally very dry and deciduous forest formations along the Pacific slope of Costa Rica below 500 m elevation; flowering and fruiting from January to June. The species ranges from Chiapas, Mexico, and the Pacific slope of Central America to Panama, Colombia, and Venezuela.

*Coccoloba caracasana* is recognized by the usually broad stiff leaves rounded at both apex and base, the short pedicels that hardly exceed the bracteoles and make the inflorescences appear to be spikes, the enlarged perianth lobes covering half the fruit, and the seasonally dry forest habitat. There is no evidence of an association with biting or stinging ants in our area. The inflorescences become pendulous with the fleshy edible white drupes, and it is from these that the common name *Papaturro Blanco* is derived.

***Coccoloba guanacastensis* W. Burger, Phytologia 49:387. 1981. Figure 24.**

Trees to over 10 m tall, leafy internodes 0–3 cm long, 1.5–4 mm thick, glabrous, becoming pale grayish and longitudinally striate; stipules (ocreae) 4–8 mm long, the distal tube 2–3 mm broad, thin and caducous, the basal portion persisting with the leaves and extending below the petiole base, glabrous. Leaves often borne close together near the ends of branches, deciduous, petioles 1.5–3 cm long, 1–2.5 mm thick, terete except near the lamina base, glabrous, becoming articulated 2–6 mm above the differentiated base of the ocrea; laminae (7) 9–23 cm long, 3–11 cm broad, broadly oblong to elliptic-oblong, obtuse to rounded at the apex and often very short acuminate, obtuse to rounded at the base, margin entire or drying undulate, the laminae drying very stiffly chartaceous and often pale grayish green in color (the newly expanded leaves drying thin and brown), smooth and glabrous on both surfaces, with 6–10 pairs of major secondary veins, the tertiary venation forming a very fine (0.2–0.6 mm) reticulum that is slightly raised on both surfaces and paler in color than the enclosed leaf areas on the lower surface (dry). Inflorescences terminal or axillary, 1 or 2 from the same node, 10–15 cm long at anthesis, clearly racemose with the flowers usually solitary (rarely 2 together) and separate along the thin (0.5–1 mm) glabrous rachis, the rachis longitudinally ridged but not thickened at the pedicel bases, the subtending bracts and bracteoles less than 0.5 mm long, deciduous, pedicels 2–4 mm long; the flowers appearing to be bisexual, 4–6 mm long and 7 mm broad, the hypanthium narrowed for 0.5–2 mm above the articulation with the pedicel, hypanthium 2–3 mm long with perianth lobes 2–3 mm long, filaments 2–3 mm long, anthers ca. 0.8 mm long, stigmas 3, exserted and thickened. Fruit (immature?) partly enclosed in the perianth base (hypanthium), perianth lobes about half the length of the developing fruit, free and separate from the upper half of the fruit; achene apparently somewhat turbinate with an expanded and rounded apical half.

Trees of the riparian forest in the seasonally very dry deciduous forest formations below 200 m elevation on the Pacific slope of northern Costa Rica; flowering from February to April. This species is known only from the province of Guanacaste in Costa Rica.

*Coccoloba guanacastensis* is recognized by the lack of pubescence, petioles articulate well above the base of the stipular sheath, minute and deciduous floral bracts, and relatively large and long-pedicellate flowers. This species appears to be closely related to *C. padiformis* and is known only from deciduous forest formations near Cañas, Bagaces, and Santa Rosa National Park.

***Coccoloba lehmannii* Lindau, Bot. Jahrb. Syst. 49:6–7. 1895. *C. changuinolana* Standl., Publ. Field Columbian Mus., Bot. Ser. 8, pt. 1:9. 1930. *C. williamsii* Standl., Field Mus. Nat. Hist., Bot. Ser. 11, pt. 5:148. 1936. *C. allenii* Lundell, Contr. Univ. Michigan Herb. 6:8. 1941. Figure 23.**

Small trees to 10 (rarely? 20) m tall, leafy internodes 2–7 cm long, 1.8–4.5 mm thick, glabrous or with resin-like excretions resembling short hairs, becoming longitudinally

striate (dry) and grayish or pale brown; stipules 5–15 (20) mm long, 1–3 mm thick, with or without glandular excretions, arising above the petiole base, caducous. Leaves alternate and distichous, petioles 8–15 (25) mm long, 1–3 mm thick, narrowly sulcate above (canaliculate) above near the lamina base, minutely puberulent, resinous punctate or glabrous; laminae (6) 9–18 (26) cm long, (3) 4.5–9 (16) cm broad, broadly elliptic to elliptic-obovate, abruptly narrowed to the acute or short acuminate apex (occasionally rounded distally), obtuse or slightly rounded at the often unequal base, margin entire or slightly undulate, drying stiffly chartaceous, smooth and glabrous above and below or minutely puberulent on the midvein, with longer crooked hairs in the axils of major veins, with 5–10 pairs of major secondary veins, the tertiary venation often subparallel and slightly raised on both surfaces when dry. Inflorescences terminal and solitary, often on short axillary shoots, 8–22 (35) cm long, peduncle 1–3 cm long, flower fascicles separate along the rachis or closely approximate but not congested, rachis 0.5–2 (3) mm thick, prominently ridged, very minutely papillate puberulent and brownish, pedicels equaling the bracteoles in length; male flowers in groups of 2–4, filaments to 2 mm long, pistil 1.5 mm long with 3 styles. Fruit enclosed in the succulent perianth, 5–7 mm long and 4–5 mm in diameter, the perianth lobes free almost to the base of the fruit, borne on pedicels to 6 mm long that clearly exceed the bracteoles; achenes 5–7 mm long, ca. 5 mm in diameter, broadest near the base and ovate in outline, strongly trigonous, pale brown to light tan and lustrous.

Trees of the wet evergreen forests of both the Caribbean and Pacific slopes between sea level and 1,000 m elevation; flowering collections have been made from March to June, and fruiting collections have been made between March and August in our area. The species ranges from central Costa Rica through Panama and Colombia to Venezuela and Peru.

*Coccoloba lehmannii* is recognized by its usually broad thin leaves, the stipule usually completely caducous to leave only a small scar on the stem, the relatively long racemes of close or separate (but not congested) flowers, and the evergreen lowland habitat. The species is known in Costa Rica from only three collections: *Dunlap 467* from along the Rio Sixaola valley, *Lent 2464* along the Rio Parismini, both in the province of Limon, and *A. Jimenez 2444* from near Golfito in southern Puntarenas province. An interesting collection with more narrowly obovate leaves has recently been made by Luis Poveda (1105) near Bijagualito-Tarcoles on the Pacific slope. This collection lacks flowers and fruit, so it is not possible to say whether it is an unusual representative of this species or perhaps a new and closely related species.

***Coccoloba obovata*** H.B.K., Nov. Gen. 2:176. 1817. *C. riparia* Lundell, Contr. Univ. Michigan Herb. 6:11. 1951. Figure 22.

Shrubs or trees 3–8 (15) m tall, leafy internodes 0.5–5 cm long, 2–4 (7) mm thick, glabrous and terete, becoming grayish or reddish brown and often splitting longitudinally when dry; stipules 5–10 (20) mm long, 3–6 mm broad, appressed and with the thin distal tube deciduous or persisting, longitudinally striate, originating 2–8 mm below the petiole and the lower portion usually persisting. Leaves alternate and distichous, petiole 0.8–4 (6) cm long, 1–3 mm thick, minutely puberulent or glabrous, striate when dry, becoming articulate 2–8 mm above the differentiated (stipular) ocrea; laminae (5) 12–22 (24) cm long, (3) 5–14 cm broad, elliptic to elliptic-obovate or occasionally ovate, tapering or occasionally rounded to the short acuminate apex, narrowed or rounded to the obtuse, truncate, or cordulate base, often unequal at the petiole with 1 side or lobe larger than the other, entire, drying chartaceous to stiffly chartaceous and usually dark above, smooth and glabrous above and below but sometimes minutely puberulent in the axils of the major veins, with 4–9 pairs of major secondary veins, tertiary veins slightly raised on both surfaces (dry), often with minute (0.1 mm) circular peltate scales on the lower surface. Inflorescences solitary and terminal, on tips of branches or short axillary shoots, 8–25 cm long, spicate or racemose and the flower fascicles densely crowded, subtended by bracteoles ca. 1.5 mm long, rachis ca. 2 mm thick, and minutely papillate-puberulent to short pilose; male

flowers borne on pedicels not exceeding the bracteoles, filaments ca. 1 mm long, anthers 0.3–0.4 mm long; female flowers on inflorescences to 17 cm long, pedicels becoming exerted only in fruit, ovary with 3 styles. Fruit included within the appressed succulent perianth, globose, or somewhat turbinate, 8–10 mm in diameter, developing thick longitudinal ribs, the free perianth lobes covering only the distal 2–3 mm of the fruit, borne on pedicels to 3 mm long and 0.5 mm thick (dry); achene difficult to separate from the enclosing perianth when dry, trigonous, tan to dark brown.

Plants of the seasonally dry partly deciduous or evergreen forest formations between sea level and 1,000 m elevation; flowering and fruiting throughout the year, but collected most often between June and September. The species ranges from the Pacific side of central Costa Rica to Panama and Colombia.

*Coccoloba obovata* is recognized by the petiole arising well above the base of the stipular tissue surrounding the node, the thin often obovate and glabrous leaves, densely flowered spikes becoming racemose in fruit, and seasonally dry but mostly evergreen habitats of the Pacific slope between the Bay of Nicoya and Chiriqui, Panama.

***Coccoloba padiformis* Meisner, in DC., Prodr. 14:166. 1856. Figure 24.**

Trees to 30 m tall, leafy internodes 2–6 cm long, 2–4 (6) mm thick, terete and glabrous, becoming pale gray; stipules 6–18 mm long, 2–5 mm broad, acute at the apex, glabrous, persisting or deciduous, becoming stiff basally, arising at about the level of the petiole attachment. Leaves alternate and usually distichous, apparently deciduous and produced in flushes, petioles 8–18 (26) mm long, 1–3 mm thick, glabrous, with a shallow adaxial groove above (canaliculate), becoming articulate at or 1–2 mm above the base of the ocreate stipule; laminae 6–18 (26) cm long, 2–8 (12) cm broad, elliptic-ovate to elliptic-oblong, tapering or rounded to the short-acuminate apex (sometimes acute or obtuse), rounded to obtuse at the base, the margin entire or slightly undulate, the edge becoming slightly revolute, the laminae drying stiffly chartaceous to subcoriaceous and often grayish or pinkish in color, smooth and glabrous on both surfaces, with 4–9 (11) pairs of major secondary veins, arcuate ascending near the margin, tertiary venation usually flat on both surfaces and obscure above. Inflorescences axillary (or terminal on very short axillary shoots?), 1–3 together, 3–8 cm long, racemose, both the male and female flowers subtended by very short (1 mm) bracts and bracteoles (ocreolae), rachis ca. 1 mm thick with minute (0.2 mm) reddish hairs; male flowers 1 or 2 per fascicle, pedicels 2–3 mm long, the hypanthium narrowed at the base (above the pedicel articulation), filaments ca. 2 mm long, anthers ca. 0.5 mm long; female flowers solitary, pistil ca. 2 mm long. Fruit included within the succulent perianth, ca. 9 mm long and 7 mm thick, free perianth lobes covering only 2–3 mm at the top of the fruit, fruiting pedicels 3–5 mm long; achene ca. 8 mm long and 6 mm in diameter, ovoid to subglobose, weakly trigonous, lustrous pale brown.

A poorly known species of evergreen or partly deciduous forests of the Pacific below 1,000 m elevation in southern Costa Rica; collected with flowers and fruit between February and April. The species ranges from the Golfo Dulce area of Costa Rica to Colombia and Venezuela.

*Coccoloba padiformis* is recognized by the glabrous vegetative parts, stiff leaves drying pale tan and with obscure tertiary venation (above), short racemose inflorescences that are usually axillary, and distinctive pedicels subtended by very small bracts and bracteoles. Included here are two collections of Paul Allen (5944 and 5964) that are said to form small stands at the heads of valleys on the summits of high (300–800 m) hills above Palmar Norte. These trees were listed under the name *C. roseiflora* Standl. & L. Wms. (never validly published) in Allen's book, *The Rain Forests of Golfo Dulce*, 1956, p. 177.

***Coccoloba tuerckheimii* Donnell Smith, Bot. Gaz. 37:213. 1904. Figure 22.**



Trees 7–15 (20) m tall, leafy internodes 0.5–4 cm long, 6–15 mm thick, often obscured by the persisting stipules, becoming striate and glabrous; stipules 2–5 cm long, overlapping near the apex of the stem, to 25 mm broad, stiffly chartaceous and striate, thicker near the base and arising below the petiole attachment, persisting with the leaves. Leaves usually clustered near the ends of branchlets, petioles 5–45 mm long, 1.5–8 mm thick, sulcate or canaliculate above, very minutely brownish puberulent or glabrescent, becoming striate or deeply ridged, borne and becoming articulate on the ocrea 6–15 (25) mm above the stipular base; laminae (13) 20–45 (70) cm long, (7) 10–25 (40) cm broad, obovate to broadly elliptic-oblong, abruptly narrowed at the short-acuminate apex, gradually narrowed at the acute or rounded base, decurrent or subtruncate at the petiole, margin entire or slightly undulate, the laminae drying stiffly chartaceous, and often dark brown, smooth and glabrous on both surfaces or minutely puberulent beneath, the axils of the major veins often with tufts of hairs, with 6–10 pairs of major secondary veins, tertiary venation slightly raised beneath and not usually subparallel (between the secondaries). Inflorescence a panicle arrangement of 10–20 racemes of nearly equal length, terminal on axillary short shoots, 20–40 cm long, the common peduncle and main axis less than 5 cm long, peduncles of the racemes less than 1 cm long, rachis very minutely (0.1 mm) puberulent and with longitudinal ridges, 1–2 mm thick and drying dark brown; male flowers in fascicles of 4–8, bracts and bracteoles 0.5 mm long or less, pedicels 2–3 mm long, filaments 1.5–3 mm long, anthers ca. 0.5 mm long; female flowers solitary, functional pistil 3 mm long. Fruit enclosed within the succulent perianth, 11–14 mm long and 6–9 mm in diameter, ovoid, the free perianth lobes covering only the apex of the fruit, the base constricted into a stalk 1–2 mm long above the pedicel articulation, fruiting pedicels 1–3 mm long; achene obtusely trigonous, dark brown.

Plants of the wet evergreen forest formations below 1,000 m elevation; fertile collections have been made in July and August. The species ranges along the Caribbean side of Central America from Guatemala to central Panama and is found in the evergreen forests of the Pacific slope in southern Puntarenas Province.

*Coccoloba tuerckheimii* is very distinctive because of the unusually large leaves borne on large striate ocreae enclosing the nodes on thick brownish stems and the panicle arrangement of long racemose inflorescence branches. Very few flowering or fruiting collections have been made of this species.

***Coccoloba uvifera* (L.) L., Syst. Nat. ed. 10:1007. 1759. *Polygonum uvifera* L., Sp. Pl. 365. 1753. Figure 21.**

Shrubs or short widely branching trees 2–8 (15) m tall, the trunk not usually straight, leafy internodes 0.3–4 (10) cm long, 2.5–10 mm thick, very minutely puberulent or sparsely glandular but quickly becoming glabrous, longitudinally striate, pale brown to gray; stipules 3–12 mm long, beginning just beneath the petiole base, very minutely puberulent to pilose, splitting as the shoot expands and becoming reddish brown. Leaves usually distichous and broader than long, petioles 5–15 mm long, 3–7 mm thick, arising just above the stipular base and becoming articulate on the ocrea, minutely papillose in ours; laminae 6–15 (18) cm long, 8–20 (27) cm broad, reniform to broadly transversely elliptic or suborbicular, often with the lateral halves unequal in area, rounded to emarginate at the apex, rounded to the cordulate or subcordate base, 1 basal lobe often extending around the petiole, margin entire, often slightly undulate with the edge revolute, the laminae thick, fleshy, and pale green when alive but drying pinkish gray and coriaceous, smooth and essentially glabrous above and below but with minute (0.05 mm) hairs on the major veins beneath and with larger hairs in the axils of the major veins, with 3–5 pairs of major secondary veins, the tertiary venation minutely reticulate or obscure, minutely punctate on both surfaces. Inflorescences usually solitary and terminal (rarely branched at the base), 15–30 cm long, racemose, the rachis ca. 3 mm thick and minutely puberulent, flower fascicles subtended by small (1–1.5 mm) bracts and bracteoles, the flower fascicles separate and not closely crowded along the rachis; male flowers in groups of (1) 2–7, pedicels 1–2 mm long, filaments 2–4 mm long, anthers 0.5–0.8 mm long; female flowers solitary, perianth 3–4 mm long. Fruit included within the succulent perianth, ca. 2 cm long



and 1.5 cm in diameter, narrowed at the base above the pedicel articulation, obpyriform to obovoid, the perianth lobes remaining free only at the top 2–4 mm of the fruit; achene difficult to separate from the perianth when dry, black at maturity.

Plants of the sandy seashore vegetation just above and behind the high water-line on both the Pacific and Caribbean coasts in Costa Rica; probably flowering and fruiting throughout the year, but with very few collections made in January or in May and June. The species ranges from Mexico and southernmost Florida (U.S.A.) through the West Indies and Central America to northern South America. This species is occasionally grown in gardens as an ornamental tree.

*Coccoloba uvifera* is distinguished by its thick stiff leaves, usually broader than long on very short petioles, thick stems with ocreae covering the nodes, long racemose inflorescences, and sandy coastal (or garden) habitats. Because the species is so characteristic of seaside vegetation and so easily recognized, it is only occasionally collected and hence poorly represented in herbaria. The plants are known as *Uva*, *Uva de Playa*, *Papaturro*, and Sea Grape in Central America. The juicy fruit is edible with a slightly acid flavor and has been used to make an alcoholic beverage in the West Indies. The hard heavy wood has been used in making furniture and for charcoal.

***Coccoloba venosa* L.**, Syst. Nat. ed. 10:1007. 1759. *Campderia floribunda* Benth., Bot. Voy. Sulphur 159, tab. 52. 1846. *Campderia mexicana* Meisner, in DC., Prodr. 14:171. 1856. *Coccoloba floribunda* (Benth.) Lindau, Bot. Jahrb. 13:217. 1890. *Coccoloba molinae* Standl. & L. Wms., Ceiba 3:198. 1952. Figure 23.

Shrubs or small trees 4–7 (10) m tall, often with a twisted trunk and thick spreading crown of many branches, leafy internodes 0–3 cm long, 2–6 mm thick, at first very minutely papillate-puberulent but quickly glabrescent, becoming pale grayish and longitudinally striate, sometimes sometimes resinous punctate, becoming lenticellate, the nodes conspicuously thicker than the internodes; stipules 5–15 mm long, originating at or just below the petiole attachment, glabrous or very minutely puberulent, deciduous or persisting with the leaves. Leaves alternate, often borne on short shoots, distichous on the long shoots, petioles 3–10 (15) mm long, 1–2.3 mm thick, glabrous or minutely puberulent, often reddish punctate or reddish brown throughout, often borne above the thickened base of the node or on the differentiated base of the ocreate stipule; laminae 5–14 (20) cm long, 2.5–7 (10) cm broad, obovate or obovate-oblong, acute to obtuse or rounded at the apex, obtuse to rounded at the base, often with small (3 mm) and unequal cordulate lobes at the petiole, entire, drying undulate and very stiffly chartaceous to subcoriaceous, smooth and glabrous above and below (in ours) except for the presence of crooked hairs in the axils of the major veins, with 5–8 pairs of major secondary veins, tertiary venation often slightly raised above and below when dry. Inflorescences usually solitary, terminal or (apparently axillary) on short axillary shoots, (4) 6–12 (16) cm long, the flowerless peduncle less than 5 mm long, flower fascicles densely crowded and the rachis often difficult to see, the rachis 1–2.5 mm thick, very minutely puberulent or glabrous, usually reddish brown and deeply ridged, basal bracts of each fascicle 1–2.5 mm long, dark and stiff, the thin bracteoles 2–3 mm long, pedicels ca. 2 mm long; male flowers several per fascicle, filaments 1–2 mm long, anthers 0.3–4 mm long; female flowers solitary, flower buds ca. 2 mm long. Fruit enclosed within the persistent slightly succulent perianth, to 6 mm long, perianth lobes separate almost to the base, narrowed at the base above the articulation with the petiole; achenes 4–5 mm long to 4 mm broad, strongly trigonous, broadest near the base and ovate or triangular in outline, dark brown and lustrous.

Plants of the seasonally very dry deciduous (tropical dry and tropical moist transition) forest formations below 200 m elevation in Costa Rica; probably flowering sporadically throughout the year, but fertile collections have been made primarily in January and February and in July and August. The species ranges from central Mexico to the northwestern Pacific lowlands of Costa Rica, and from

Hispaniola and Puerto Rico southward through the Lesser Antilles to Trinidad and Venezuela.

*Coccoloba venosa* is recognized by the short-petiolate obovate-oblong leaves borne on thick grayish stems with thickened nodes, compact spikes with densely crowded flowers, and deciduous lowland habitat. The species is occasionally found near the seashore. Common names that have been used for the species in our area include *Papaturro*, *Papaturro de Playa*, *Papaturro Negro Macho*, *Papaturro Rastero*, and *Gateador*.

## MUEHLENBECKIA Meisner

### Nomen Conservandum

Small shrubs, slender climbers, or lianas, unisexual or bisexual, stems mostly glabrous and longitudinally striate; stipules united to form a thin tube (ocrea) surrounding the stem, deciduous or persisting. Leaves alternate and simple, sessile or petiolate; laminae entire, glabrous. Inflorescence basically fasciculate and axillary, often racemose or spike-like with the fascicles alternating along leafless stems or the stems branched and paniculate, the flowers occasionally borne directly from the axils of persisting leaves; fascicles subtended by thin stipule-like (ocreolate) bracts. Flowers unisexual (in ours) or bisexual, borne on short pedicels articulate at the base of the perianth, perianth usually deeply 5-lobed (rarely 4- or 6-lobed), segments subequal, united near the base to form a shallow cup, stamens 8 (9), inserted on the perianth cup, filaments free, anthers introrse, staminodes present or absent in the female flowers, a pistillode present or absent in the male flowers; ovary 3-angled, style 3, short, stigmas fimbriate to capitate. Fruit remaining enclosed in the persistent perianth, the perianth becoming somewhat larger and slightly succulent in many species; achenes trigonous, the edges rounded or acute, the surface often dark and lustrous.

A genus of about 20 species best represented in montane and southern South America, New Zealand, and Australia. The genus is characterized by woody climbing or clambering stems (or subshrubs of high mountains), very small flowers in small fascicles, and five tepals that enlarge just enough to enclose the fruit and become slightly fleshy.

- 1a Distal stems flat and ribbon-like; leaves usually absent; flower fascicles borne alternately along the edges of the phyllodes just above transverse lines; cultivated ornamentals or occasional escapes ..... *M. platyclada*
- 1b Stems terete or angular; leaves always present ..... 2a
- 2a Large shrublike plants with clambering or climbing stems to over 3 m long; leaves often cordulate at the base, to 12 cm long; flower fascicles in spikelike or paniculate arrangements; 1,500–3,000 m ..... *M. tamnifolia*
- 2b Small subshrubs with stems less than 80 cm long; leaves elliptic, to 10 mm long; flowers solitary or fasciculate in the leaf axils; plants of high montane paramo vegetation above 3,000 m ..... *M. volcanica*

**Muehlenbeckia platyclada** (F. v. Muell.) Meisner, Bot. Zeitung 23:313. 1865, as *platyclados*. *Polygonum platycladum* F. v. Muell., Trans. & Proc. Philos. Inst. Victoria 2:73. 1858. *Homalocladum platycladum* (F. v. Muell.) Bailey, Gentes Herb. 2:58. 1929.

Shrubs, 0.5–3 m tall, with many closely crowded branches, glabrous, unisexual, basal and primary stems terete, the distal stems flat and straplike, less than 1 mm thick (dry) and 5–15 mm broad, with distinct transverse lines ca. 1–2 cm distant and demarking the nodes, the surface with closely parallel ribs 0.2–0.5 mm apart; stipules (ocreae) represented by a transverse line across the flattened stem. Leaves usually absent, sessile; laminae 2–5 cm long and 0.5–1.5 cm broad, cuneate to hastate at the base, narrowly lanceolate distally, acute at the apex, glabrous, quickly caducous. Inflorescences small flower fascicles borne alternately along the edges of the stems just above the transverse

lines, pedicels ca. 1 mm long; flowers small and unisexual, perianth ca. 2 mm long. Fruit included within the sweet red succulent perianth, ca. 5 mm long; achene ca. 3 mm long.

Unusual plants native to the southwestern Pacific and adjacent areas. These plants are often grown in gardens and in pots for their dense branching and unique stems. They escape and grow in the wild on occasion, but do not appear to persist in our area. The flat stems with transverse line and small flower fascicles alternating along the edges of the distal phyllodes distinguish this species from virtually all other terrestrial plants. The species is often called *Solitaria* or *Tenia* in Spanish and "Ribbon Bush" or "Tapeworm Plant" in English.

***Muehlenbeckia tamnifolia*** (H.B.K.) Meisner, Gen. Pl. 2:227. 1840. *Polygonum tamnifolium* H.B.K., Nov. Gen. & Sp. 2:180. 1817. Figure 19.

Woody vines or lianas, scrambling or climbing to 15 m high, often forming dense masses, unisexual or bisexual, glabrous, leafy internodes 0.5–3 (8) cm long, 0.8–4 mm thick, often with 2 or 4 longitudinal ridges, drying reddish brown and striate; stipules tubular (ocrea), thin and translucent, 5–15 mm long but often deciduous, entire distally, leaving a distinct scar around the stem. Leaves alternate and usually distichous, slightly succulent when alive, glabrous, petioles 4–16 (20) mm long, with 2 adaxial ridges continuous with the lamina margins; laminae 3–9 (12) cm long, 1–4 (6) cm broad, elliptic-oblong to elliptic-ovate or elliptic, tapering gradually or abruptly to the acute or acuminate apex, usually rounded near the base and auriculate or cordulate with a relatively wide sinus or the laminae sometimes gradually tapering to an obtuse or acute base (rarely auriculate and acute on the same plant), margin entire, usually drying thin chartaceous, venation pinnate with 7–14 pairs of major secondary veins, the basal secondaries often dichotomizing halfway to the margin. Inflorescences 1–3 from the axils of leaves, simple and racemose or spikelike or branched and panicle (sometimes with reduced leaves), unisexual or bisexual, very variable (2–15 cm) in length, flowers in alternating fascicles subtended by a number of ocreolate bracts 1–3 (5) mm long, rachis 0.3–0.6 mm thick, pedicels 0.5–3 mm long and articulate beneath the perianth. Flowers unisexual, small, pale yellowish to greenish white, the perianth usually 5-parted, united near the base, ovate; male flowers ca. 2 mm long, stamens 8 (10), borne on the lower half of the tepals, ca. 1 mm long, anthers ca. 0.5 mm long, a pistillode present or absent; female flowers 1.5–3 mm long, ovary 3-angled, styles 3 and spreading, stigmas fimbriate, staminodia usually present. Fruit loosely enclosed within the persistent perianth, perianth enlarging slightly to cover the fruit; achenes bluntly 3-angled, 2.5–3.5 mm long, 2–3 mm broad, dark and lustrous.

Vinelike plants of evergreen moist and wet montane forest formations, from (1,400) 1,800 to 2,900 (3,100) m elevation in Costa Rica; probably flowering throughout the year, but collected most often between September and March. This species is known from southern Mexico and Guatemala, central Costa Rica to western Panama, and western South America.

*Muehlenbeckia tamnifolia* is recognized by the clambering stems with annular scars left by the ocreate stipules, thickened nodes with reddish brown surfaces, glabrous leaves often cordulate at the base, and the small fasciculate flowers in spikelike or panicle-like inflorescences. Plants placed under this name exhibit an interesting polymorphism as regard the shape of the leaf base. In Costa Rica, about one-third of the collections have an acute or obtuse leaf base, while the majority have a slightly auriculate or cordulate leaf base. The latter often have a conspicuous (2–5 mm) basal bract with dark midvein subtending the flower fascicles, whereas plants with acute leaf bases seem to lose these bracts early or to have them less well developed. The plants with acute leaf bases also seem to have their inflorescences more often branched. A closer examination of these differences in the field might prove rewarding.



**Muehlenbeckia volcanica** (Benth.) Endlicher, Gen. Pl. Suppl. 4:51. 1847. *Polygonum volcanicum* Benth., Pl. Hartweg. 81. 1841.

Small shrubs or dwarf shrubs, 5–50 cm tall, stems to 75 cm long, usually prostrate or pendent, leafy internodes with conspicuous ridges, very minutely puberulent; stipules with a tube 1–2 mm long. Leaves alternate, closely spaced, petioles 0–3 mm long; laminae 3–10 mm long, 2–5 mm broad, elliptic to rhombic-elliptic, tapering gradually to both acute apex and attenuate base, drying coriaceous. Flowers axillary, solitary or in fascicles, pedicels very short, flowers 2–3 mm long, greenish white. Fruit fleshy and black, loosely enclosed in a calyx 3–4 mm long; seed an ovoid-trigonus achene.

Plants found only on Costa Rica's highest mountains above 3,100 m elevation, but ranging from 2,400 to 4,000 m in Guatemala. The species ranges from southern Mexico to Guatemala, Costa Rica and Colombia to Bolivia.

*Muehlenbeckia volcanica* is recognized by its very small stature, tubular ochreate stipules, very small leaves, and high altitude habitat. Arthur Weston's careful collecting on Chirripó in 1976 first disclosed the presence of this species in Costa Rica.

### PODOPTERUS Humboldt & Bonpland

Shrubs or small trees, bisexual, branches usually terminating in stiff spines, leaves and inflorescences usually borne on small rounded short shoots (spur shoots or brachyblasts); ochreate stipules small, caducous. Leaves alternate in a spiral or in fasciculate clusters on small axillary short shoots, deciduous and the plants leafless for much of the year, lamina thin and entire, venation pinnate. Inflorescences fascicles of flowers borne on small axillary short shoots, pedicels articulate. Flowers bisexual and regular, small, perianth of 2 whorls of 3 parts, united near the base, the outer 3 perianth parts larger and each with a longitudinal keel along the midrib that quickly expands to form a thin wing decurrent on the pedicel, the inner smaller perianth whorl with flat erect parts enlarging slightly in fruit; stamens 6, free, filaments filiform, anthers ovate; ovary trigonous, styles 3, stigmas capitate, ovule basal and sessile. Fruit a trigonous achene, included within the persisting and enlarged perianth, each of the 3 outer perianth parts with a thin expanded longitudinal wing arising from the back (abaxial) side of midrib, the wing rounded near the apex of the perianth part and long-decurrent on the pedicel.

A genus of three species previously known only from Mexico, Belize, and Honduras. The genus has a number of unusual characters, including spiny branches with small rounded short shoots, deciduous leaves usually borne in fascicles, flowers and fruits also in fascicles borne on the rounded short shoots, and fruit with persisting perianth and unusual wings that are decurrent on the pedicels. The genus is only found in deciduous formations with a severe dry season.

**Podopterus mexicanus** Humboldt & Bonpland, Pl. Aequin. 2:89. 1812. Figure 20.

Shrubs or small trees, 2–5 (8) m tall, usually branched near the base of or with a short trunk, stems straight or angled and with short rounded spur shoots and terminal spines, leafy internodes 0.3–2 cm long, 1.5–5 mm thick, smooth and usually dark gray in color, glabrous; ochreate stipules not usually apparent, stipule scars encircling the young stems often difficult to see, older stems with the stipule scars obscure except near the leaf base. Leaves usually borne in fascicles of 2–5 on short shoots ca. 3 mm long, deciduous, petioles (3) 5–20 mm long, ca. 0.6 mm thick, minutely puberulent with very short (0.1–0.2 mm) straight hairs; laminae 2–7 cm long, 1.5–4.5 cm broad, broadly elliptic to obovate, rounded to bluntly obtuse at the apex, gradually narrowed to the cuneate base, margin entire, laminae drying stiffly chartaceous, smooth on both surfaces, glabrous or very minutely puberulent along the midvein beneath, the 3–6 pairs of major secondary veins arising at



an angle of ca.  $50^\circ$  from the midvein. Inflorescences fascicles of flowers borne on short (3–4 mm) thick short shoots (brachyblasts) alternate along the stems, with 5–20 flowers per fascicle, pedicels articulate near the base; flowers small and said to be green but becoming white and with the 3 outer perianth parts soon developing longitudinal wings along their midribs. Fruit borne within the thin whitish to pale brown or yellowish pink perianth parts, 2–3 cm long including the pedicel, wings of the outer 3 perianth parts 2–3 mm broad and 10–15 mm long, decurrent on the pedicels for 5–10 mm, the wings thin and translucent, achene ca. 5 mm long and 3 mm broad, with 3 narrow longitudinal ribs, the surface pale brown and lustrous.

Trees and shrubs of the dryest seasonally deciduous woodlands and scrub formations along the Pacific side of Central America between sea level and 700 m elevation; fruiting collections have been made from late December to March. The species ranges from central Mexico through western Guatemala and Honduras and has recently been collected in northwestern Costa Rica.

*Podopterus mexicanus* is recognized by the spine-tipped branches with alternating rounded short shoots (spur shoots), small fasciculate leaves rounded at the apex and cuneate at the base, the small fasciculate white flowers, and the fruit with outer perianth parts bearing broad thin wings that are long-decurrent on the pedicel. The restriction to seasonally very dry areas and the (often obscure) stipule scars further distinguish these plants. They are called *Escambron* and *Escambron negro* in Honduras. This species was not known from Costa Rica until early December 1977, when Daniel Janzen collected it growing near the swamp at Palo Verde, Guanacaste. A collection by William Haber (74) from the same locality was made on March 17, 1977.

### POLYGONUM Linnaeus

Herbs, climbers or rarely shrubs, annual or perennial, bisexual, often growing in or near water, stems often with thickened nodes and longitudinal ridges, glabrous to strigose and occasionally with gland-tipped hairs; stipules and leaf base developed into a tubular leaf sheath that surrounds the stem and is called an ocrea, the ocrea often with cilia or stiff awns on its distal margin. Leaves alternate and simple, some species articulate above the leaf sheath, subsessile to short-petiolate; laminae linear to ovate and occasionally cordate to sagittate or hastate, margins entire, glabrous or puberulent, usually pinnately veined, often glandular or pellucid punctate. Inflorescences basically fasciculate, the flowers in the axils of leaves or leaflike bracts but more often subtended by ocrea-like bracts that are borne close together on a raceme-like or spikelike axis, the flowering axes solitary or several in a panicle-like arrangement, terminal or axillary near terminal leaves, flowers borne on pedicels articulated near their apex. Flowers bisexual or occasionally functionally unisexual, radially symmetrical, small, perianth of 4–6 subequal tepals in 1 or 2 whorls, the inner often smaller and of thinner texture, perianth united near the base, green to white or pink and red in color, imbricate in bud and persisting in fruit; stamens (3) 5–8 (9), often unequal in length, included or protruding on filaments free or adnate to the perianth near the base, anthers small, introrse, usually isodiametric and versatile (appearing peltate); ovary superior, lenticular or trigonous, styles 2 or 3 and united near the base, stigma small and capitate, locule 1 with an erect basal ovule. Fruit an achene, lenticular or trigonous, ovate to orbicular in outline, usually included in the dry persisting perianth, the apex often beaked with a persistent style base, surface of the fruit often dark and lustrous.

A genus of about 150 species often growing in open wet habitats and with the great majority of species in the North Temperate Zone. With the exception of the common *Polygonum punctatum*, the Costa Rican species of the genus are poorly represented in collections. This is probably due to the fact that most live in wet habitats that collectors have difficulty working in. Additionally, populations are quite variable, and delimitation of species is often difficult. The genus is seriously

in need of monographic revision, and one suspects that a great many species will have to be redefined as much broader concepts than those currently in use.

Most of our species of *Polygonum* are easily recognized by their herbaceous habit, narrow alternate pinnately veined leaves, flowers in spikelike or raceme-like inflorescences, and the very unusual stipular structure (ocrea) enclosing the node. Some Commelinaceae have similar stipular developments, but their leaves are not pinnately veined.

- 1a Flower groups borne on long (1.5–15 cm) spikelike or raceme-like axes; common plants ..... 2a
- 1b Flowers in small groups in the axils of leaves or on short (0.5–1.5 cm) raceme-like or spikelike groups at the ends of much longer slender flowerless peduncles; plants rarely collected in Costa Rica ..... 6a
  - 2a Outer perianth parts and/or the ocreate bracts subtending the flowers with distinctive minute (0.1 mm) disklike gland dots; flower fascicles often somewhat separate on the flowering rachis; leaves gradually narrowed to apex and base; a common species ..... *P. punctatum*
  - 2b Outer perianth parts and ocreate floral bracts lacking disklike gland dots; flower fascicles often crowded on the floral rachis; less common species ..... 3a
  - 3a Distal margins of the ocreae (stipular tube above the leaf base) with very short (1–2 mm) setae or ciliate awns or these lacking; plants rarely with conspicuous hairs, pubescence often confined to leaf margins and midveins, stems often slender; leaves usually narrow and tapering gradually to apex and base ..... 4a
  - 3b Distal margins of the ocreae with long (2–20 mm) stiff setae, plants often conspicuously pubescent, lower stems often more than 1 cm thick; fruit lenticular ..... 5a
    - 4a Distal branches of the inflorescence lacking minute gland-tipped hairs, flower fascicles often somewhat separate on the flowering rachis; fruit lenticular or trigonous; mostly from the Caribbean lowlands (in ours) *P. hydropiperoides*
    - 4b Distal branches of the inflorescence with minute gland-tipped hairs, flower fascicles usually crowded; fruit lenticular with 2 flat faces ..... *P. segetum*
  - 5a Stems and inflorescence branches with longer strigose hairs and minute gland-tipped hairs; green leaflike flanges often present on the distal margin of the ocreate stipules; laminae somewhat rounded near the base ..... *P. hispidum*
  - 5b Stems and inflorescence branches with appressed ascending strigose hairs, gland-tipped hairs absent; stipules with setae to 25 mm long but lacking flanges; laminae tapering gradually to the base ..... *P. acuminatum*
  - 6a Laminae broadly ovate to triangular and deeply cordate, petioles usually more than 1 cm long; introduced vining weeds of open sites, naturalized in a few areas in Panama but not recorded from Costa Rica and not included in the species descriptions ..... *P. convolvulus*
  - 6b Laminae never broadly ovate or deeply cordate, (rarely subcordate to hastate), petioles less than 5 mm long; plants erect or clambering but not vines ..... 7a
  - 7a Laminae 5–15 cm long; flowers clustered in fascicles at the ends of long slender inflorescence branches; native plants of swamps and marshes, 0–1,800 m *P. meisnerianum*
  - 7b Laminae 0.5–4 cm long; flowers in fascicles in the axils of leaves; introduced weeds of short (less than 0.5 m) stature, 1,500 m and above ..... *P. aviculare*

***Polygonum acuminatum* H.B.K., Nov. Gen. & Sp. 2:178. 1817. *P. guatemalense* Gandoger, Bull. Bot. Soc. France 66:225. 1919. Figure 17.**

Herbs to 1.5 (rarely 2) m tall, usually erect, leafy internodes 2–4 (12) cm long, 4–8 (15) mm thick, with appressed ascending strigose hairs but soon becoming glabrous; stipules 1–4 cm long with a usually dense covering of slender ascending hairs 1–4 mm long, distal margin with 10 or more stiff setae (awns) 10–25 mm long; leaves alternate in a spiral, subsessile or with petioles 1–15 mm long, lateral margins of the petioles continuous with

the lamina margins, appressed strigillose; laminae 8–23 (30) cm long, 1.5–3.5 (5) cm broad, narrowly lanceolate to linear-lanceolate, occasionally curved and falcate, tapering gradually to the acuminate or acute apex, gradually tapering to the base and abruptly decurrent on the petiole, margin entire and densely strigillose, laminae drying chartaceous and smooth to the touch, the surfaces usually covered with appressed hairs distally oriented and 0.1–1 mm long, the hairs often more dense along the midvein and margins, venation pinnate with 13–25 pairs of major secondary veins. Inflorescences terminal or axillary from near-terminal leaves, to 30 cm long, raceme-like or spikelike with a single axis or with 1–3 branches and panicle, primary peduncle (2) 4–7 cm long, appressed strigose, branches of the inflorescence 6–16 cm long with the flowering portion (1) 3–11 (14) cm long, ca. 1 cm in diameter at full anthesis, fascicles of flowers closely crowded and partly overlapping, bracts of the fascicles 2–3 mm long and with distal cilia 0.5–2 mm long, pedicels exceeding the bracts by 1–2 mm; flowers ca. 3–4 mm long, whitish or pink, perianth united only near the base, usually 4-parted, stamens usually 6 and becoming exerted beyond the perianth, anthers ca. 0.5 mm long, versatile, styles 2, 2–3 mm long. Fruit a thick lenticular achene 2–2.5 mm long, ovate in outline and with convex faces, dark brown or black, lustrous.

Plants of swamps, streamsides, wet depressions, and dense aquatic (rooted or floating) vegetation from sea level to about 1,500 m elevation; probably flowering throughout the year in Central America. The species ranges from southern Mexico and the West Indies to southern South America.

*Polygonum acuminatum* is characterized by the often robust stems, general presence of thin ascending appressed (strigillose) hairs, long-setose stipules, ciliate floral bracts, crowded flower fascicles, and thick lenticular fruit. The species is known from only two collections in Costa Rica: *Brenes* 14353 from near San Ramon, Alajuela, and *Standley* 48465 from near Cairo, Limon province.

### ***Polygonum aviculare* L., Sp. Pl. 362. 1753.**

Annual herbs, prostrate or decumbent-ascending, simple or much branched, often densely leafy with short internodes, leafy internodes 0–10 (30) mm long, 0.5–1.5 (3) mm thick, smooth and glabrous, often ridged or angled and becoming longitudinally striate when dry; stipules forming short (2–5 mm) tubular ocreae, the ocreae very thin and translucent, smooth and lustrous, becoming lacerate distally. Leaves alternate in a spiral, often bluish green in color, glabrous, clearly articulate just above the sheathing ocreate base, subsessile or very short (0–3 mm) petiolate; laminae 0.5–3 (4) cm long, 1.5–5 (8) mm broad, very narrowly elliptic to narrowly elliptic-oblong, bluntly acute at the apex, acute and decurrent on the base, margin entire, laminae drying stiffly chartaceous, venation pinnate with 3–5 pairs of major secondary veins. Inflorescences of fasciculate flowers in the axils of leaves or leaflike bracts, 1–5 flowers per fascicle, pedicels to 2 mm long; flowers 2–3 mm long, perianth greenish white to pinkish or white, tepals rounded at the apex, fruit a 3-angled achene, ovate in outline, dark brown, dull or slightly lustrous.

A weed of roadsides and open ground originally from north temperate areas but now naturalized at higher altitudes in the tropics. The species is known in Costa Rica from only three collections, all from the southern slope of Volcan Irazu near Tierra Blanca, Cartago.

*Polygonum aviculare* is recognized by its small narrow leaves, many-branched and often procumbent stems, translucent ocreae on the leaf bases, articulate small narrow leaves, flowers in axillary fascicles and usually open weedy habitat. This species has become naturalized in Guatemala, where it probably does not persist below 1,500 m elevation; it is not likely to be found in our area below 1,500 m.

### ***Polygonum hispidum* H.B.K., Nov. Gen. & Sp. 2:178. 1817. Figure 17.**

Herbs, 0.5–1.5 m tall, perennial and often with robust viscid stems to 2 cm thick, leafy internodes 1–8 cm long, 3–10 mm thick, usually densely strigose to hispid with stiff pale-colored hairs 2–6 mm long and minute (0.2–0.5 mm) reddish gland-tipped hairs;



stipules forming a narrow tube 2–20 mm long with setae on the distal margin 2–5 mm long and often with distal rounded reflexed or spreading flanges, long ascending and minute gland-tipped hairs covering the surface. Leaves alternate in a spiral, petioles 1–6 cm long with lateral ridges continuous with the lamina margins, strigose-hispid and with gland-tipped viscid hairs; laminae 7–30 cm long, 3–12 cm broad, ovate-triangular to narrowly ovate-elliptic or broadly lanceolate, tapering gradually to the acute or acuminate apex, abruptly rounded near the base but gradually decurrent on the petiole, margin entire and strigose, the laminae drying thin chartaceous, smooth to the touch but strigose-hispid along the veins above and below, usually glabrous between the veins on older leaves, venation pinnate with 10–25 pairs of major secondary veins, the lower surface punctate. Inflorescences to 30 cm long, usually panicle with 3 flowering branches, the primary peduncle 5–10 (15) cm long and ca. 3.5 mm thick, branches 4–16 cm long and bearing flowers over more than half their length, flowerless axes of the inflorescence with strigose hairs 1–2 mm long and minute gland-tipped hairs, flower fascicles congested or closely approximate, spikelike and raceme-like, 6–18 mm thick, fascicles subtended by ocreate bracts 3–4 mm long, bracts usually with few hairs on the back and a ciliate margin of stiff hairs 0.5–1 mm long, pedicels becoming slightly longer than the bracts; flowers 3–5 mm long, deep pink to dark red (rarely greenish), perianth lobes 5, stamens 5, filaments 1.5–2 mm long, styles 2 and ca. 2 mm long, united for half their length. Fruit a lenticular achene, 3–4 mm long, ovate to orbicular in outline, with 2 flat or slightly concave faces, becoming black or very dark brown, lustrous, style persisting and ca. 1 mm long.

Plants growing in and along streams and in seasonally wet swampy sites from sea level to 1,500 m elevation; flowering throughout the year in Central America, but collected most often in August. The species ranges from Guatemala and the West Indies to southern South America.

*Polygonum hispidum* is recognized by the combination of larger strigose or hispid and minute gland-tipped hairs, the unusual herbaceous flanges on the stipule-margins (not always developed), the larger laminae rounded above an attenuate base, the colorful flowers, and the lenticular fruit. In living material, the stems and leaves are usually viscid. Virtually all the Central American collections come from the Pacific slope, but the species has not yet been collected in Costa Rica. The plants are called *Tobacon* and *Tobaquillo* in Honduras.

***Polygonum hydropiperoides* Michaux, Fl. Borealis 1:239. 1803. Figure 17.**

Herbs, to ca. 1 m tall, lower stems usually slender and often rooting at the nodes, leafy internodes 0.5–6 cm long, 1–4 mm thick, glabrous or with a few minute strigillose hairs, becoming longitudinally striate when dry; stipules forming a narrow tube 8–20 mm long, the distal margin entire or with small (1–2 mm) thin setae (ciliate awns). Leaves alternate in a spiral, petioles 2–5 mm long and not clearly differentiated from the lamina; laminae 5–12 (15) cm long, 0.4–1 (1.5) cm broad, very narrowly elliptic or elliptic-lanceolate to linear-lanceolate, tapering very gradually to the acute apex, tapering very gradually to the attenuate base, margin entire and minutely strigillose, laminae drying chartaceous and smooth to the touch, minutely (0.1–0.5 mm) strigillose on the midveins and margins and often glabrous between, venation pinnate with 10–18 pairs of major secondary veins, pellucid-punctate in transmitted light. Inflorescences to ca. 15 cm long, panicle or unbranched, the spikelike or raceme-like flowering portions 1–5 cm long and 0.5–1 cm in diameter, ocreate bracts subtending the fascicles 2–3 mm long; flowers 2–3 mm long, pedicels becoming ca. 1 mm longer than the subtending bract; flowers 2–3 mm long, usually 5-parted, the outer perianth lobes 1.5–2 mm long, white or pink, stamens usually 8, anthers less than 0.5 mm long, ovary trigonous or lenticular, styles 2 or 3. Fruit a 3-angled or lenticular achene (mostly lenticular in Costa Rica), 2–3 mm long and ca. 1.5 mm broad, ovate in outline, brown to black, becoming lustrous.

Plants of river edges, wet depressions, and sandy or gravelly soils near water; flowering throughout the year, but seen most often during the wet season. Although these plants grow from sea level to 1,500 m elevation on the Pacific side of northern Central America (El Salvador, Honduras, and Guatemala), they have



only been collected from below 200 m on the Caribbean slope in Costa Rica and Panama. The species ranges from the southern United States to South America, where it appears to merge with *P. persicarioides*.

*Polygonum hydropiperoides* is recognized by the almost glabrous aspect of the plants, the slender stems, the narrow leaves tapering gradually to both apex and base, slender inflorescences with flower fascicles not closely crowded, and fruit that may be either lenticular or trigonous. As used here, *P. hydropiperoides* includes Central American material previously identified as *P. persicarioides* H.B.K. Specimens placed here may include individuals of *P. punctatum* lacking the characteristic gland dots on perianth and floral bracts. Likewise, specimens of *P. segetum* lacking gland-tipped hairs may find themselves placed under this name. The use of *P. hydropiperoides* as something of a catchall is, I believe, justified by the very poor state of our knowledge of these semiaquatic plants in Central America. James S. Wilson has annotated specimens of this species as *P. persicaria* L. in the herbarium of the University of Wisconsin; a Linnean epithet may be the ultimate repository for this material.

***Polygonum meisnerianum* Cham. & Schlecht., Linnaea 3:40. 1828. Figure 17.**

Herbs, to ca. 1 m tall, decumbent or somewhat scandent, leafy internodes 1–5 (8) cm long, 1.2–3 mm thick, glabrous or with stiff retrorse barbs or prickel-like hairs (these often at the base of the node), occasionally with gland-tipped hairs; stipules narrow and tubular, 8–30 mm long, distally with short (1–2 mm) setae or entire, glabrous or with strigose or glandular hairs. Leaves alternate in a spiral, sessile or with petioles 1–4 mm long, retrorse hairs covering the petiole or only along the adaxial ridges continuous with the lamina margins; laminae 5–15 cm long, 0.6–1.6 (2) cm wide, linear lanceolate, tapering very gradually to the acute apex, abruptly narrowed at the base (very rarely subcordate or hastate at the base in Central America), margin entire and with minute (0.1–0.2 mm) ascending and/or glandular hairs along the edge, the laminae drying thin-chartaceous, with stiff curved retrorse or ascending hairs to 1 mm long on the midvein beneath or occasionally scattered over the leaf surface, venation pinnate with 15–30 pairs of major secondary veins. Inflorescences terminal, panicles 5–20 cm long, primary peduncles 2–8 cm long, glabrous or with minute gland-tipped hairs, usually branching dichotomously, usually with 2–5 thin branches 1–8 cm long and bearing flowers only in the distal 10–16 mm, branches of the inflorescence subtended by minute small ocreate bracts and with few to many minute gland-tipped hairs; flowers ca. 3–4 mm long, borne on pedicels not exceeding the floral bracts, perianth lobes less than 2 mm long, usually white. Fruit ca. 3 mm long, 3-angled, ovate in outline, lustrous pale brown, with a short (0.2 mm) beak.

Plants of lake edges, swamps, and marshes from 500 to 1,800 m elevation in Central America and apparently flowering throughout the year. The species ranges discontinuously from central Mexico to Brazil and the West Indies.

*Polygonum meisnerianum* is distinctive because of its open few-branched panicles with relatively few (1–5) flower-fascicles at the ends of long thin secondary peduncles. The glandular hairs usually found on the secondary peduncles and the stiff retrorse hairs on leaves and nodes further distinguish this species. Only two collections have been seen from Costa Rica; one from Lago Arenal, Guanacaste (A. Jimenez 2699), and the other from Cañas Gordas, Puntarenas (Pittier 11089). The aquatic habitat of this species probably accounts for the fact that so few collections have been made in our area.

***Polygonum punctatum* Elliott, Sketches Bot. S. Carol. & Georgia 1:445. 1817. *P. acre* H.B.K., Nov. Gen. & Sp. 2:179. 1817. Figure 17.**

Herbs to ca. 1 m tall, annual or perennial, often with creeping stems, leafy internodes 0.5–2 (4) cm long, 1.3–10 mm thick, glabrous or rarely with ascending appressed strigose hairs, longitudinally ridged when dry, partly included in the tubular stipule of the previous node; stipules tubular and narrow, (5) 12–25 mm long, glabrous or rarely with appressed hairs, the distal margin setose ciliate with hard yellowish setae (bristles or awns) 2–8 mm long (rarely smaller). Leaves alternate in a spiral, petioles 1–10 (15) mm long, gradually merging with the sheathing ocreate (stipular) base and enclosing the stem; laminae (2) 4–10 (17) cm long, (0.5) 1–2 (4) cm broad, very narrowly elliptic to lanceolate or linear-lanceolate, tapering gradually to the acute or acuminate apex, decurrent on the petiole, margin entire and minutely (0.3 mm) strigose, the laminae drying chartaceous and slightly rough to the touch, usually glabrous above except for the margins and midvein, glabrous below or with appressed ascending (strigose) hairs on the major veins, hairs ca. 0.2–0.5 mm long, venation pinnate with 5–15 (25) pairs of major secondary veins, the lamina pellucid punctate when viewed by transmitted light. Inflorescences solitary or less often 2–3 from the axils of near-terminal leaves, spikelike or raceme-like with a single major axis or occasionally with 1 or 2 branches and paniculate, 5–20 cm long, flowering portion 2–10 (15) cm long and ca. 0.5 cm thick, flower fascicles separate along the axis and not closely crowded, fascicles subtended by tubular ocreate bracts ca. 2–3 mm long, entire or awned apically, usually glandular punctate; flowers exerted from the bracts on slender (0.2 mm) pedicels, ca. 4 mm long and articulate at the apex, flowers ca. 3–4 mm long, gradually narrowed to the base, perianth lobes ca. 2 mm long, glabrous but with raised pellucid dots, white to pale greenish in color, the 3 larger outer parts imbricate and including the 2 inner perianth parts; stamens usually 8, filaments 1–1.5 (2) mm long, anthers less than 0.5 mm in diameter, subglobose, ovary trigonous, style ca. 1 mm long, connate basally. Fruit a 3-angled achene (in ours), ovate in outline, 2.5–4 mm long, 1.5–2 mm broad, dark brown to black and lustrous, beak inconspicuous.

Herbs of wet depressions in open areas, moist forest edges, and stream sides from sea level to 2,000 m altitude; flowering throughout the year in Costa Rica, but with most of the collections made between December and April and in July and August. This species ranges from southern Canada to Argentina and is found in Asia.

*Polygonum punctatum* is readily recognized among our species by the pellucid punctate perianth and floral bracts. The species is further distinguished by the narrow leaves tapering gradually to both apex and base and the inflorescences with flower fascicles never closely crowded. This is the most commonly encountered species of *Polygonum* in Central America and often referred to as *Chile de perro* in Costa Rica. This species is very similar to *P. hydropiperoides* among our species; *P. hydropiper* L. of north temperate areas is a closely related species. *Polygonum punctatum* is variable over its wide range, and a number of varieties have been proposed (see Norman Fassett, The variations of *Polygonum punctatum*, Brittonia 6:363–393, 1949).

***Polygonum segetum*** H.B.K., Nov. Gen. & Sp. 2:177. 1817. *P. mexicanum* Small, Bull. Torrey Bot. Club 19:256. 1892. Figure 17.

Herbs to ca. 1 m tall, mostly annuals, sometimes decumbent, leafy internodes (0.5) 2–9 cm long, 1.3–6 (10) mm thick, smooth and glabrous or rarely with gland-tipped hairs, somewhat longitudinally striate when dry; stipules tubular and narrowly enclosing the stem, 5–35 mm long, glabrous, entire or with a few short (1 mm) cilia distally. Leaves alternate in a spiral, petioles 2–15 mm long, with lateral margins continuous with the lamina margins, sparsely short-strigose; laminae 5–16 cm long, (0.5) 1–2.5 cm broad, linear to lanceolate, occasionally curved and falcate, tapering very gradually to the acute or acuminate apex, tapering gradually to the base and decurrent on the petiole, margin entire but with appressed ascending minute stiff hairs along the edge, laminae drying chartaceous, usually with minute (0.1–0.4 mm) appressed ascending stiff hairs on the major veins, margins and near the tip, glabrous and minutely punctate between the veins,

venation pinnate with 10–30 pairs of major secondary veins. Inflorescences solitary or less often 2 or 3 from the axils of near-terminal leaves, spikelike or raceme-like with a single major axis or occasionally with 1 or 2 branches and paniculate, to 20 cm long, flower-bearing rachis 1–6 cm long, 8–18 mm thick, primary peduncle and inflorescence branches usually with minute (0.1–0.3 mm) gland-tipped hairs, flowers in crowded fascicles subtended by ocreate bracts 2–4 mm long, bracts entire distally or with very short (1 mm) thin cilia, glabrous or minutely gland punctate, pedicels equaling or slightly exceeding the bracts; flowers 3–4 mm long, to 5 mm in fruit, pale pink or white, outer perianth lobes 2–2.5 mm long, ovary lenticular, styles 2. Fruit (2) 3–4 mm long, 2–3 mm broad, orbicular in outline, lenticular with 2 flat faces, pale brown becoming very dark brown or black, lustrous.

Aquatic or semiaquatic plants of lake edges, wet depressions, seasonally flooded land or occasionally forming floating mats on open water; between sea level and 1,500 m elevation and probably flowering throughout the year, but collected most often in November and from January to March. The species ranges from Mexico to Colombia and the Greater Antilles.

*Polygonum segetum* is distinguished by the glandular hairs on peduncles, flowers often closely grouped on the floral axes, lenticular fruit, narrow leaves that taper gradually to apex and base, and preference for aquatic and temporarily flooded habitats. Specimens lacking the distinguishing gland-tipped hairs will key out to *P. hydropiperoides*, and that species may prove to be a catchall for a variety of atypical material. Vegetatively, the plants are also similar to *P. punctatum*, with appressed ascending hairs usually confined to the major veins and margins of the leaves.

*Polygonum mexicanum* is placed under *P. segetum* following C. D. Adams in the Flowering Plants of Jamaica (1972). The plants placed here are also closely related to *P. pennsylvanicum* L. of the eastern United States.

### RHEUM Linnaeus

Herbs, with thick woody rhizomes, aerial stems short (1 m) or lacking; stipules thin and loose, without cilia. Leaves often large, petiolate, the laminae palmately veined, often sinuately dentate or palmately lobed. Inflorescences panicles with small clusters of flowers; the flowers bisexual or functionally male, perianth 6-parted, subequal or the outer whorl smaller, not enlarging in fruit; stamens usually 9, anthers ovate; ovary trigonous, styles 3, short and recurved. Fruit an achene, narrowly or broadly 3-winged, embryo straight.

A genus of about 30 species best represented in eastern Asia and originally ranging to eastern Europe. A few are cultivated for their large showy leaves and one (*Rheum rhabarbarum*) is widely grown as a vegetable for its succulent petioles which are used with sugar as a vegetable or a filling for pies.

#### *Rheum rhabarbarum* L., Sp. Pl. 372, 1753.

A large perennial herb, most of the leaves borne from the base of the rhizome and lacking a prominent stem but producing inflorescences to 2 m tall. Leaves to 1 m long, the petiole thick and succulent, often reddish in color; laminae broadly ovate to suborbicular, 50–80 cm broad, deeply cordate at the base, the margin undulate, glabrous, venation palmate with usually 5 primary veins. Inflorescences 1–2 m tall, a narrowly pyramidal leafy panicle, flowers small and pale green to white, on slender articulated pedicels, similar to those of *Rumex*.

Rhubarb (*Ruibarbo*) is cultivated at middle elevations in Costa Rica; the reddish succulent petioles are often seen in vegetable markets of the Meseta Central. The name *Rheum rhaponticum* L. has been used for this species, but refers to a species of Bulgaria that is little cultivated.



## RUMEX Linnaeus

REFERENCE: K. H. Rechinger, Die süd- und zentralamerikanischen Arten der Gattung *Rumex*. Ark. Bot. 26, no. 3:1–58. 1934.

Perennial herbs, rarely annual or woody shrubs, unisexual or bisexual, glabrous or sparsely puberulent, stems often longitudinally striate and hollow; stipules united to form a sheathing tube (ocrea) around the stem, usually very thin and translucent, persistent but lacerate and withering. Leaves alternate, simple, often dimorphic with basal or lower cauline leaves differing from those near the inflorescences, early leaves often forming basal clusters, petioles sheathing the stem at their base and united with the ocreae; laminae entire or minutely dentate, often slightly succulent. Inflorescences racemose or paniculate but basically composed of flower fascicles borne along an unbranched axis (and these axes usually in panicle-like arrangements), the fascicles at first enclosed in stipule-like (ocreolate) bracts, the flowers sometimes numerous within the fascicle and appearing to be verticillate or whorled, the flowers borne on simple or articulate (ebracteolate) pedicels. Flowers bisexual or unisexual, mostly wind-pollinated, radially symmetrical, the perianth of 6 parts in 2 whorls of 3 each, the outer whorl usually smaller than the inner whorl and reflexed, remaining small, the inner 3 perianth parts usually larger and often enlarging in fruit, both whorls persisting in fruit, stamens 6, free, filaments very short, anthers 2-theous, narrowly oblong, usually longer than the filaments; ovary 3-angled (trigonous), styles 3 and spreading or reflexed, stigmas fimbriate or penicillate, locule and ovule 1. Fruit usually enclosed within the stiff dry persisting perianth parts of the inner whorl, in some species at least 1 of the enlarged perianth parts develops a grainlike tubercle on the back (abaxially) of the midrib; fruit a 3-angled achene, the 3 longitudinal ribs usually acute, the surface smooth and lustrous or rough and dull.

A genus of perhaps 200 species, most of which grow in the Northern Hemisphere. The genus is recognized by the very thin stipules encircling the stem, the leaves often varying in form on the same stem, the small flowers often in verticill-like groups along the inflorescence branches, perianth parts in two whorls of three with the parts persistent and closely enclosing the fruit. In some species, at least 1 of the inner perianth parts enclosing the achene develops a grainlike tubercle on the back of the midrib. This remarkable and conspicuous (pale colored) structure may serve as a seed-mimic and reduce predation on the achenes. Of the four species represented in Costa Rica, three are widely naturalized weeds recognized by Linnaeus over 200 years ago, while the fourth species is a unique high-mountain endemic that may include the tallest plants known in the genus.

- 1a Flowers borne on pedicels becoming 3 cm long; plants regularly becoming more than 2 m tall, stems to 10 cm thick at the base; usually found only in moist protected sites above 2,800 m elevation. . . . . *R. costaricensis*
- 1b Flowers borne on pedicels usually less than 1 cm long; plants rarely becoming more than 1.5 m tall . . . . . 2a
- 2a Small plants only occasionally becoming 50 cm tall; leaves 1–5 cm long, basal leaves often with divergent lobes (hastate); flowers unisexual, 2 mm long or less; fruiting perianth without grainlike tubercles on the back of the midrib; 1,500–3,500 m elevation  
*R. acetosella*
- 2b Larger plants regularly becoming 50 cm or more tall, leaves 2–40 cm long, basal leaves never hastate; flowers bisexual, usually more than 2 mm long; fruiting perianth often with a grainlike tubercle developed on the back of the midrib . . . . . 3a
- 3a Enlarged sepals (valves) with entire margins in fruit, without sharp projections or spines, flowers and fruit often crowded on the inflorescence axis; largest basal leaves usually less than 4 cm broad, rarely truncate or subcordate; common weeds, 1,000–2,000 m . . . . . *R. crispus*
- 3b Enlarged sepals with spine-like projections along the edge in fruiting stages; flowers and fruits often in separate verticils along the flowering rachis; larger leaves commonly truncate to cordate; uncommon weeds, 1,000–2,800 m elevation. . . . . 4a
- 4a Enlarged sepals with a few straight spines along the margin; larger leaves usually more



- than 5 cm broad, broadest below the middle, laminae margins arising at about the same level on the petiole. . . . . *R. obtusifolius*
- 4b Enlarged sepals with distinctly hooked (uncinate) spines along the margins; larger leaves 2–10 cm broad and often broadest at the very base of the laminae, margins usually arising 1–5 mm distant along the apex of the petiole . . . . . *R. nepalensis*

***Rumex acetosella* L., Sp. Pl. 338. 1753. Figure 18.**

Perennial herbs 10–40 (60) cm tall, usually branched only at the inflorescence and near the base, spreading by slender rootstocks, usually unisexual, glabrous, leafy internodes 0–3 cm long, with 6–9 distinct longitudinal ribs; stipules 0.5–1 cm long, thin and translucent, lacerate. Leaves often dimorphic with basal and distal leaves of different form, petioles weakly differentiated from the laminae, 4–40 mm long, with lateral margins continuous with the laminae margins; upper (distal) laminae 1–3 cm long, 1–4 mm broad, very narrowly elliptic and tapering gradually to both apex and base, lower (basal) laminae 1–5 cm long, often with divergent basal lobes (hastate), lanceolate or narrowly elliptic to obovate above the basal lobes and 2–12 mm broad, acute to obtuse at the apex, usually attenuate on the petiole below the divergent lobes, margins entire, the laminae drying chartaceous, (often slightly succulent and with a pleasant sour taste in life), venation subpalmate with usually 3 major veins. Inflorescence usually a panicle of spicate branches (a simple spikelike or raceme-like axis on small plants), usually unisexual, the flowers borne in fascicles resembling verticels on the inflorescence branches, each fascicle subtended by an ocreate (stipule-like) bract and with 1–6 (9) flowers, the flowers borne on slender pedicels 0.5–3 mm long. Male flowers 1–2 mm long, perianth of 3 narrow outer parts and 3 inner slightly broader parts, a pistillode absent. Female flowers 0.5–1.5 mm long, outer perianth parts small and narrow, the inner perianth parts broader and expanding in fruit, ovary strongly 3-angled, the fimbriate stigmas ca. 0.5 mm long. Fruit included within the persistent perianth, larger perianth parts ca. 1.5 mm long and closely appressed to the fruit, entire; achene 1–1.5 mm long, 3-angled, surfaces flat or convex, ovate to orbicular in outline, smooth, dull or slightly lustrous, brown.

Introduced weeds of open and disturbed sites at higher elevations. In Costa Rica, the plants are commonly found between 2,200 and 3,500 m elevation and occasionally down to 1,500 m; flowering and fruiting throughout the year. The species, a native of Europe and Asia, is now widely naturalized.

*Rumex acetosella* is recognized by its often hastate basal leaves that are usually slightly succulent and have a pleasant sour taste. The small stature, very small reddish flowers and fruit, and open weedy high-altitude habitats further distinguish this species. The plants are often called *Ruibarbillo* in Central America. This species and its close relatives have sometimes been placed in a separate genus, *Acetosella*.

***Rumex costaricensis* Rechinger, Repert. Sp. Nov. 40:300. 1936. Figure 18.**

Large single-stalked herbs 2–5 (7) m tall, bisexual, glabrous, the main stems usually unbranched below the flowering nodes, leafy internodes to 15 cm long, 5–10 cm thick, hollow, longitudinally striate, glabrous and smooth; stipules (ocreae) to 18 cm long and surrounding the stem (at upper nodes), thin and translucent, pale reddish brown, with many subparallel veins. Leaves alternate in a spiral, somewhat polymorphic with the upper leaves on the plant attenuate to the stem and the lower leaves petiolate and rounded near the base, petioles 0–3 cm long near the inflorescence and 2–12 cm long lower on the stem, 3–10 mm broad, with lateral margins continuous with the laminae margins; laminae 20–60 cm long, 5–15 cm broad, narrowly elliptic, tapering gradually to the acute or acuminate apex, gradually tapering to the attenuate base (distal laminae near the inflorescence) or abruptly rounded at the base (more basal cauline leaves), margin entire (sometimes very slightly undulate), the laminae drying thin chartaceous, smooth and glabrous above and below, venation pinnate with 20–40 pairs of major secondary veins. Inflorescence paniculate, terminal or 1–3 from the axils of leaves, bisexual, flowers borne in fascicles of 10 or more, separate and distant along the flowering axes, inflorescences

usually with many male and few female flowers; the flowers unisexual and glabrous, borne on long (to 3 cm) slender pedicels. Male flowers 4–7 mm long, the outer tepals 1.5–2 mm long, inner tepals 4–6 mm long, stamens with very short filaments, anthers 2.5–3.3 mm long, a small pistillode present. Female flowers ca. 2–3 mm long, inner perianth whorl ca. 2 mm long, ovary ca. 1 mm long with fimbriate styles 0.5–1 mm long. Fruit loosely enclosed within the persisting perianth, larger perianth parts becoming 4–6 mm long, and 2–5 mm wide, emarginate; achene ca. 3 mm long (immature?), strongly 3-angled, with convex faces ca. 2 mm broad and broadly ellipsoid in outline, becoming dark greenish brown.

Unusual plants apparently restricted to partly open sites on moist slopes and stream edges in areas protected from strong winds and found only from (2,200?) 2,800 to 3,400 m elevation; probably flowering throughout the year, but collected with flowers and fruit only from December to March and in June and July. The species is endemic to Costa Rica and known only from the Cerro de las Vueltas (Heredia) and on the Cerro de la Muerte (along the Interamerican Highway bordering the provinces of San Jose and Cartago).

*Rumex costaricensis* is recognized by its tall single-stalked habit, hollow thin-walled stems, large leaves with many veins, large tissue-thin stipules, and paniculate inflorescences to 50 cm long. This is one of Costa Rica's most unusual high-mountain endemics and seems to be restricted to very moist areas subject to wet Caribbean winds. This species apparently attains the largest size known for the genus and is closely related to *R. peruanus* Rech. and *R. tolimensis* Wedd. of the high Andes of northern South America.

***Rumex crispus* L., Sp. Pl. 335. 1753. Figure 18.**

Erect perennial herbs 0.3–1.5 m tall, with a thick taproot, the stems usually unbranched below the inflorescence, bisexual, leafy internodes 1–5 (10) cm long, 3–10 mm thick, glabrous, longitudinally striate, hollow; stipules 0.5–5 cm long, thin and translucent. Leaves quite variable on the individual plant, often forming dense clusters at the base of the plant, petioles 1–5 cm long (to 10 cm on basal leaves); clasping the stem at the base; laminae 3–25 cm long, 0.5–4 cm broad, linear-lanceolate to narrowly oblong or linear-oblong, acute at the apex, attenuate at the base (rounded or cordate on basal leaves), margin undulate and crisped, minutely crenate-dentate, the laminae drying chartaceous, smooth and glabrous above and below, venation pinnate with 10–20 pairs of major secondary veins. Inflorescences terminal and paniculate with racemose branches or axillary and racemose, the flowers in verticil-like fascicles on the flowering axes, the verticils (whorls) closely approximate, and subtended by ocrea-like bracts, flowers borne on slender pedicels 1–5 (12) mm long; flowers bisexual, outer tepals 1–2 mm long and not expanding in fruit, oblong, inner tepals ovate to cordate and becoming 3–5 mm long in fruit, stamens 6 with filaments less than 0.5 mm long, anthers 1–3 mm long, ovary 3-angled, stigmas fimbriate. Fruit tightly enclosed within the persisting perianth, the perianth parts 3–5 mm long and ca. 3 mm broad in fruit, entire, often with an expanded ellipsoid tubercle ("grain") on the base of the midrib abaxially becoming 3 mm long and 1.5 mm broad; achene 1.5–3 mm long, ca. 1.3 mm broad, 3-angled with 3 flat or slightly convex faces, ovate to orbicular in outline, lustrous dark brown.

Introduced weeds from Europe and naturalized in areas of extensive agricultural and similar activity. The species has only been collected in the Central Highlands (around the Meseta Central) between 1,000 and 2,000 m in Costa Rica; flowering and fruiting material has been collected from December to May and in August. The species is now naturalized in many parts of the world.

*Rumex crispus* is recognized by the densely flowered inflorescences, undulate and obscurely dentate leaves, and the entire perianth parts which (in the inner whorl) enlarge in fruit and often have a grainlike development on their back (abaxially). The young leaves are eaten after cooking in the United States, but this

practice is not recorded from Central America. The plants are called *Lengua de vaca*, *Lengua de caballo*, and *Lechugon* in Guatemala.

***Rumex nepalensis*** Sprengel, Syst. Veg. ed. 16, 2:159. 1825. Figure 18.

Herbs, 0.3–1 m tall (in ours), leafy internodes 0–10 cm long, 1.5–6 cm thick, glabrous, longitudinally ribbed; stipules thin and soon tearing off. Leaves basal or cauline but not differing greatly in form, petioles 1.5–10 cm long; laminae 5–15 (21) cm long, 1.5–5 (10) cm broad, ovate-oblong to narrowly triangular and broadest at the base, acute to bluntly obtuse at the apex, truncate to cordate or somewhat hastate at the base, margins entire and usually arising 1–5 mm distant on the petiole, laminae drying thin-chartaceous with 9–15 pairs of major secondary veins. Inflorescences terminal or axillary, 10–50 cm long, the flower fascicles 5–12 mm distant on the deeply ridged glabrous rachis, the fascicles forming verticil-like (whorled) clusters with short (1–4 mm) pedicels articulated near the base; flowers ca. 2 mm long at anthesis. Fruit enclosed in valves (enlarged sepals) 3–5 (6) mm long and with numerous hooked (uncinate) spines 1–3 mm long on the margins, the tubercles (grains) on the abaxial surface poorly developed or absent but the venation prominent.

An apparently recently introduced weed collected only in San Jose (*Godfrey* 67336) and on the grounds of the University (*Croat* 593 and 959), both in 1965. These specimens are smaller in almost every respect than those seen from other parts of the world, but the valves with their hooked spines are diagnostic.

***Rumex obtusifolius*** L., Sp. Pl. 335. 1753. Figure 18.

Erect perennial herbs, 0.5–1.5 m tall, often forming dense colonies, bisexual, leafy internodes 0–8 cm long, 2–8 mm thick, longitudinally striate, glabrous; stipules (ocreae) to 5 cm long, very thin, pale yellowish and translucent. Leaves often polymorphic on the same plant, the basal leaves often in dense clusters and long-petiolate, petioles 1.5–15 cm long, 0.5–3 mm broad, clasping the stem at their base; laminae 4–25 (40) cm long, 1–10 cm broad, tapering gradually to the acute apex, the upper (distal) laminae elliptic to lanceolate or ovate-elliptic and tapering to the obtuse base, the lower (basal) laminae much larger and oblong to ovate-oblong, truncate to cordate at the base, margin entire or crisp-undulate and minutely crenate-dentate in larger leaves, the laminae drying thin-chartaceous, smooth and glabrous above, minutely (0.2 mm) puberulent on the veins beneath (the trichomes rather thick and irregular), venation pinnate with 4–14 pairs of major secondary veins. Inflorescences racemose or paniculate, the flowers borne in somewhat separate verticil-like fascicles, the fascicles subtended by ocreate bracts, the flowers borne on articulate pedicels to 8 mm long. Flowers bisexual, 2–3 mm long, the 3 outer perianth parts ca. 0.5 mm broad, the inner parts broader (1–1.5 mm) and longer (2–3 mm), enlarging and developing unusual lobes in fruit, anthers ca. 1.5 mm long, stigmas fimbriate. Fruit tightly enclosed in the persisting and enlarged perianth, inner perianth parts (valves) 3–7 mm long, with narrow or teethlike lobes along the margin, an ellipsoid tubercle (grain) 2–3 mm long often developing on the back of the midrib; achene 2–3 mm long, strongly 2-angled with 3 convex faces, ovate or elliptic in outline, lustrous brown, the perianth becoming reddish.

Introduced weeds of open sites in montane habitats between 1,200 and 2,800 m elevation; probably flowering primarily in the wet season and early part of the dry season (June to February). Native of Europe and Asia and now widely naturalized.

*Rumex obtusifolius* is recognized by the raceme-like inflorescences, with separate whorls (actually fascicles) of flowers, articulate pedicels, unusual teeth and thickened "grains" on some of the fruiting perianth parts, and the long-petiolate basal leaves. The stems are said to be eaten for stomach ailments in Costa Rica.

#### RUPRECHTIA Meyer

REFERENCE: A. E. Cocucci, Revision del Genero *Ruprechtia*, Kurtziana 1:217–269. 1961.



Trees or shrubs, unisexual (dioecious), stems solid; stipules forming a tube around the stem (ocrea), small and thin, caducous or evanescent. Leaves alternate and simple, deciduous, petiolate, the laminae pinnately veined, glabrous or puberulent. Inflorescence racemose or of racemose axes in a panicle arrangement on a leafless terminal twig, the flowers borne in fascicles subtended by several thin ocreolate bracts, the flowers pedicellate (in ours), flowers very small at anthesis. Male flowers with 3 sepals, free or united at the base, usually obtuse and membranaceous, the 3 inner petals (tepals) similar to the sepals and alternate with them; stamens 9, the outer whorl with 6 stamens in pairs alternating with the petals and the inner whorl of 3 stamens opposite the petals, a disk usually present, a pistillode absent. Female flowers with 3 sepals, free or united and with or without a conspicuous tube, greatly enlarging in fruit, 3 petals alternate with and much smaller than the sepals, glabrous or pilose, 9 very small staminodes usually present; ovary with 3 short styles and 3 globular or linear stigmas. Fruit retained within the persisting perianth, the sepals always enlarging in fruit, often with 3 long narrowly spatulate wings, stiffly chartaceous in texture; achene with 3 deep longitudinal sulci separating the rounded faces of the fruit, narrowly ovoid to ellipsoid and narrowed to the persisting styles and stigmas, seed deeply 3-sulcate.

A New World genus of 17 recognized species, with several species in Mexico and a majority in southern South America. These separate centers of diversity probably reflect the fact that most of the species are restricted to seasonally dry and deciduous habitats. These plants are recognized by the small flowers in fasciculate groups subtended by ocreolate bracts, the unusual three-winged fruit very similar to those in *Triplaris*, and the restriction to seasonally very dry areas of northwestern Costa Rica. In addition to the differences listed in the key, *Ruprechtia* differs from *Triplaris* in chromosome number ( $n = 14$  in *Ruprechtia* and 11 in *Triplaris*) and the much smaller stipules that are often difficult to see.

***Ruprechtia costata*** Meisner, in DC., Prodr. 14:180. 1857, sensu lato. *R. deamii* Robinson, Proc. Amer. Acad. Sci. 43:51. 1907. *R. kellermanii* Donn. Smith, Bot. Gaz. 47:260. 1909. Figure 20.

Medium-sized to tall trees, 2–10 (25) m tall, trunk to ca. 35 (60) cm in diameter, unisexual, leafy internodes 0.3–1.5 (5) cm long, 0.7–2 (5) mm thick, at first with thin ascending hairs ca. 0.5 mm long, soon becoming glabrous and gray, lenticellate; stipules forming a short (1 mm) thin tube around the stem and leaving a very obscure ring around the stem. Leaves usually distichous, articulate at the base (below the ocrea), petioles 2–6 mm long, with lateral margins continuous with the lamina margins; laminae 3–11 (18) cm long, 1.5–5 (8) cm long, elliptic or slightly elliptic-obovate to elliptic ovate, tapering to a short-acuminate apex (in ours), acute to obtuse at the base, margin entire or slightly undulate-crenate, the laminae drying chartaceous (in ours) or subcoriaceous, glabrous above and with few thin ascending hairs on the midvein beneath, the midvein prominent above and below, venation pinnate with 5–7 (11) pairs of major secondary veins. Inflorescences racemose, 1–3 from the axils of leaves or fallen leaves, occasionally in panicle arrangements on leafless stems, flower fascicles subtended by small (1 mm) thin-translucent ocreolate bracts, flowering axes to ca. 3 cm long in ours (to 10 cm in others). Male flowers on puberulent pedicels 1–2 mm long, perianth ca. 2 mm long, filaments ca. 3 mm long, anthers ca. 0.6 mm long; female flowers not seen. Fruit enclosed within the enlarged dry perianth and borne on pedicels 2–4 mm long, pedicel and perianth with thin erect hairs 0.2–0.5 mm long, fruiting perianth 2–4 cm long, (only 2–2.5 cm long in ours with wings ca. 15 mm long and 3–4.5 mm wide), pale rose brown when dry; achene becoming 1 cm long, 3–4 mm thick with 3 deep longitudinal sulci separating the 3 rounded sides of the fruit, narrowly ovoid to ellipsoid and usually puberulent on the upper half.

Trees of the seasonally very dry deciduous (tropical dry) forest formations of Guanacaste province below 300 m elevation; flowers and fruit have only been collected in January, February, and March. The species ranges from Guatemala to the Pacific lowlands of northern Costa Rica and central Panama.



*Ruprechtia costata* is recognized by its distinctive 3-winged fruiting perianth with the texture of stiff paper and basal tube loosely enclosing the 3-furrowed achene. The ocreate stipules are very small and difficult to see, while the male inflorescences are densely (though often minutely) puberulent, with the flower fascicles subtended by a cluster of small thin ocreolate bracts. The fruiting perianth resembles that of *Triplaris*, but does not enclose the fruit so tightly.

The current usage of the name *Ruprechtia costata*, following Cocucci, includes specimens of diverse aspect. Specimens from Guatemala with subcoriaceous leaves to 18 cm long, with long male inflorescences and fruiting perianth to 4 cm long are quite different from the Costa Rican material with thin leaves, male inflorescences usually only about 2 cm long, and fruit becoming only 2.5 cm long. In addition, our material has foliage with fewer secondary veins. There are Guatemalan collections that appear to be intermediate between these extremes; more collections are needed to ascertain the importance of these variations. Our material from Guanacaste is closely matched by specimens from Mexico identified as *R. pringlei* Greenman, a species not treated in the recent monograph. (Earlier, our material had been placed under the name of a South American species, *R. cumingii* Meissn.)

### TRIPLARIS Loefling

Trees, unisexual (dioecious), distal stems and branches hollow and often populated by fiercely stinging or biting ants, young stems densely strigose to glabrescent; stipules united and forming a cap over the shoot apex (as in *Ficus*), leaving a raised annular scar around the stem at each node, the annular ridges often present on older stems (5–10 cm in diameter), the stipular structure (ocrea) united to the petiole only at the base, deciduous. Leaves alternate and usually distichous, folded (plicate) in bud, short-petiolate, the laminae generally elliptic to ovate or oblong, often unequal at the base, entire, strigose or sericeous to glabrescent, venation prominent beneath, the younger leaves often with longitudinal striae or folds reflecting the development within the bud. Inflorescence basically an unbranched axis (spicate or racemose), the spikes or racemes in groups of 1–8 in the axil of a leaf or undeveloped leaf, often in alternate groups on a terminal twig on which the leaves fail to develop or are soon deciduous and thus forming a panicle-like compound inflorescence, the flowers usually in fascicles (male) or solitary (female), at first enclosed in ocrea-like bracts (ocreolae), the bracts opening along the adaxial side and soon deciduous, the flowers unisexual, subsessile to short-pedicellate, often densely sericeous or strigose on the outside, regular. Male (staminate) flowers 1–5 per fascicle, tepals 6, linear to ovate, uniseriate and equal or subequal, stamens 9, exceeding the tepals on slender filaments, anthers versatile, introrse, 4-theous, a pistillode absent. Female (pistillate) flowers pedicellate and mostly solitary, perianth of 2 very different series, an outer sepaloid series of 3 broad thin parts that are united to form a distinct tube in the lower  $\frac{1}{2}$ – $\frac{1}{4}$ , the inner series of 3 very narrow stiff perianth parts free or partly adnate to the tube and equal to or only slightly exceeding the length of the tube, the perianth strongly accrescent in fruit with the 3 outer lobes becoming spatulate to oblanceolate paperlike wings, staminodes absent or forming an annular disk (rarely with functional stamens), ovary strongly 3-angled with acute edges, styles 3 with stigmatic areas on their inner faces, locule 1, ovule 1. Fruit an achene included within the persistent and enlarged 3-winged perianth tube, the achene usually 3-angled and ovate in outline, the surfaces lustrous or dull, occasionally verrucose or pustulate.

A neotropical genus with probably fewer than 20 species, most of which are confined to South America. These trees are quite distinctive, with large colorful compound inflorescences, fruit enclosed in a three-winged papery perianth, stipules capping the shoot apex and leaving raised scars around the stems, and the frequent presence of aggressive ants. Several species of the genus are planted as ornamental trees.

Variability of the populations, apparent intergradation of what have been called species, and lack of monographic study in the last 100 years have made this a particularly difficult genus. I have simplified the Costa Rican situation by adapting Duke's excellent treatment for the Flora of Panama and assuming that *T. cumingiana* finds its northern limit in westernmost Panama. Since no specimen from Costa Rica can be unambiguously keyed to *T. cumingiana* (following Duke), the decision to exclude that species from our account is, I believe, justified. Our material will probably prove to be the northern element of a more broadly circumscribed species, such as *T. cumingiana*.

**Triplaris melaenodendron** (Bertol.) Standley & Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. 23:5. 1943, *Velasquezia melaenodendron* Bertoloni, Fl. Guatem. 40. 1840. *T. macombii* Donn. Sm., Bot. Gaz. 19:257. 1894. Figure 20.

Trees, 5–15 (25) m tall, unisexual, trunk with circular annular rings in early stages, the bark flaking off in broad flat patches, biting or stinging ants often present in the hollow distal stems, leafy internodes 1–4 (8) cm long, 3–10 mm thick, with thin appressed and ascending strigose hairs but soon becoming glabrous, often reddish brown in color, longitudinally striate; stipules 1.5–3.5 (5) cm long, densely strigose on the outer surfaces, leaving an annular scar around the stem, caducous. Leaves usually distichous, articulate at the base, longitudinally folded in bud, petioles 4–20 mm long, 2–5 mm thick, strigose abaxially and along the 2 lateral margins, glabrous in the upper (adaxial) shallow sulcus; laminae 15–35 cm long, 6–18 cm broad, ovate-elliptic to ovate-oblong, acute or very short acuminate at the apex, rounded to the obtuse and often unequal base, entire, the laminae drying chartaceous to stiffly chartaceous, smooth or very slightly scabrous above, glabrous or sparsely strigose above, strigose beneath with thin stiff hairs 1–2 mm long on the major and minor veins, venation pinnate with (12) 14–20 pairs of major secondary veins. Male inflorescences spikelike, 1–8 from the axil of a leaf or fallen leaf, often panicle-like when leaves have fallen or are undeveloped on terminal twigs bearing spikes, the spikes 10–25 cm long, flowers borne in fascicles at first enclosed in narrowly ellipsoid or narrowly ovoid bracts borne spirally on the rachis of the spike, rachis and bracts usually densely yellowish brown strigose, the primary floral bracts deciduous and each fascicle producing several flowers; male flowers ca. 5 mm long, perianth of 3 linear and 3 narrowly deltoid tepals united near the base, filaments to 7 mm long, anther 0.5–1 mm long. Female inflorescence basically a compact raceme, solitary or paired, usually borne in leafless axils on a terminal twig and paniculate in form, the spikelike racemes 5–20 cm long, the compound terminal inflorescence to 40 cm long, the flowers solitary and at first enclosed in narrowly ovoid bracts (resembling the stipules), bracts and rachis densely strigose with yellowish brown hairs 1–2 mm long, bracts ca. 1 cm long and narrowed at the base, deciduous, flowers solitary from within the bract on short pedicels; female flowers 10–15 mm long at early anthesis, pedicels and outer perianth surface densely strigose or sericeous, ovary ca. 3 mm long, strongly 3-angled. Fruit an achene tightly enclosed and united near the base to the dry persisting long-winged perianth, fruiting perianth 4–6 cm long, perianth tube ca. 14 mm long and 8 mm thick, the wings 3–5 cm long, oblanceolate, 6–10 mm broad, thin chartaceous, venation pinnate and raised on both surfaces, the 3 wings usually parallel and not spreading, the inner perianth parts adnate to the tube for 4–7 mm from the base; achene ca. 11 mm long and 7 mm broad, ovate in outline and strongly 3-angled, the faces slightly convex (deeply concave when undeveloped) and lustrous dark brown, tightly enclosed by the perianth tube (especially near the base) and difficult to free from the tube, style short, style branches usually breaking off.

Trees of both the seasonally very dry deciduous forest formations and the wet evergreen formations of the Pacific slope from near sea level to 300 (850) m elevation in Costa Rica; usually flowering in January and February and with fruit in February and March. The species, as presently defined, ranges from central Mexico to southernmost Costa Rica; however, these plants will probably prove to be the northern representatives of a more broadly defined South American species (see below).

*Triplaris melaenodendron* is readily recognized by its large panicle-like compound inflorescences, bright pinkish red or reddish brown fruit with three long papery wings, the hollow distal stems usually inhabited by aggressive little ants, the shoot apex at first enclosed in a stipule that leaves a prominent scar around the stem, the rather large leaves with numerous secondary veins, and the bark on older trees breaking off in flakes or strips. This species appears to intergrade with *T. cumingiana* Fischer & Meyer, and some of our collections may be intermediates between the two (*A. Jimenez* 3799, *Molina et al.* 18245, *Skutch* 4242; all from the General Valley). *Triplaris cumingiana* differs in having somewhat narrower leaves with a greater number of secondary veins and with the inner perianth parts adnate for only 2–5 mm on the pistillate perianth tube. All these plants will probably prove to be subspecific elements of more broadly defined species. Considering the present state of knowledge, I believe it best to follow Duke's treatment in the Flora of Panama (*Ann. Missouri Bot. Gard.* 47:353–359, 1960); see also the remarks by Standley & Steyermark in the Flora of Guatemala (*Fieldiana, Bot.* 24, pt. 4:136–137. 1946).

Common names used in Central America for these trees are *Canilla de Mula*, *Callito*, *Hormigo*, *Mulato*, *Tabaco*, *Tabaco de Monte*, *Tabacon*. The name *Mulato* refers to the patchy, variously colored bark. The Brunka name is *Turi-Svan-Kra*. Many of our collections come from along streams and in flood plains, but it may be that these individuals have more accessible lower branches than those growing in forests. Included among the collections placed here is a form (*Allen* 5923 and 6012) with larger fruiting perianth and whitish trunk; see the remarks in Paul Allen's book, *The Rain Forests of Golfo Dulce* (1950, p. 348).

## CHENOPODIACEAE

Herbs (in ours), shrubs, or rarely small trees, bisexual or unisexual, glabrous or puberulent, sometimes with inflated or flattened hairs, the stems frequently semisucculent, often with anomalous anatomy; stipules absent. Leaves alternate, less often opposite or whorled, simple, often becoming conspicuously smaller and narrower on distal stems, often slightly succulent (reduced to scales in some genera), sessile or petiolate, margin entire to lobed or with conspicuous teeth. Inflorescences often of condensed cymes of few closely approximate or appressed flowers (glomerules), the glomerules often borne on distal axillary or terminal unbranched (spikelike) or branched (panicle-like or thyrselike) stems, glomerules often subtended by reduced leaves, the flowers often subtended by a bract and bracteoles; flowers bisexual or unisexual, usually small and radially symmetrical, perianth of 1 whorl and calyx-like, thin or semisucculent, of 2–5 parts (rarely absent or 1), free or united near the base, persisting in fruit, stamens as many as the perianth parts or fewer, opposite the perianth parts, free or united at the base to the perianth or to a disk, filaments flattened to filiform, bent inward in bud, anthers dorsifixed and introrse, 2- or 4-thecous, pollen polyporate; ovary superior or united at the base to the perianth or disk, 1-locular, with 1 basal ovule borne on an erect funicle. Fruit a utricle, often tightly enclosed within the persisting perianth or bracts, indehiscent (rarely circumscissile); seed variously oriented within the fruit, and with much endosperm, embryo strongly curved, annular to hippocrepiform (circular to horseshoe-shaped), rarely spiral or conduplicate.

A large family well represented in deserts, semideserts, and saline environments of the Northern Hemisphere, especially common in eastern Europe and western Asia. The family is poorly represented in the tropics, and none of its species seem to be members of Costa Rica's indigenous flora. The slightly succulent or edible alternate leaves, small greenish flowers with stamens borne at the base of the sepals, lack of petals, sessile stigmas, solitary locule with ovule borne on a basal funicle, and smooth lenticular seeds help distinguish our species. The



strongly curved embryo surrounding much endosperm is a characteristic of the order Centrospermae, also called the Chenopodiales or Caryophyllales. Our species are easily confused with members of the Aizoaceae and some Amaranthaceae.

- 1a Plants growing wild, herbaceous weeds of open sites; basal and lower leaves rarely more than 10 cm long; flowers not subtended by bracts or bracteoles; fruit loosely enclosed in the dry slightly enlarged and separate perianth parts . . . . . *Chenopodium*
- 1b Plants cultivated for food and ornament; basal leaves often exceeding 15 cm in length; flowers subtended by small bracts; fruits tightly enclosed within the united perianth parts or bracts . . . . . 2a
- 2a Flowers bisexual; plants cultivated for the edible root, edible leaves or colorful leaves; fruit enclosed by the hard and woody perianth, bracts and bracteoles remaining free (*Acelga*, *Remolacha*) . . . . . *Beta*
- 2b Flowers unisexual, plants cultivated for the edible leaves; fruits enclosed in a nut-like structure formed by the 2 subtending bracts and often with spines (*Espinaca*) . . . . . *Spinacia*

### BETA Linnaeus

Herbs, annual, biennial or perennial, roots often thick and fleshy. Leaves whorled or in a rosette at the base, alternate on the stems, laminae entire or sinuate, venation pinnate. Inflorescences small clusters of flowers, solitary in leaf axils or terminal, often on distal spikelike or paniculate branches, a bract and 2 bracteoles subtending each flower; flowers bisexual, small, greenish or reddish, perianth urceolate and 5-lobed, united at the base to the ovary and to other flowers, becoming stiff in fruit, stamens 5, borne on the side of the ovary, anthers oblong, ovary united to perianth and stamens near the base and appearing to be sunken into a disk, with 3 (2–5) short stigmas. Fruit enclosed within the hardened and nearly closed perianth, often the product of several flowers united together, pericarp free of the seed and united to the perianth at the base; seed horizontal (with the long axis at right angles to the floral axis), orbicular to reniform, embryo annular or subannular.

A genus of about 12 species native to northern Africa, Europe, and Asia. This genus includes the many cultivated varieties of beets grown for their nutritious roots, the leaves used for green vegetables, and, in some varieties, the colored foliage for ornamental plantings.

#### *Beta vulgaris* L., Sp. Pl. 222. 1753.

Herbs, annuals, stems to 1.3 m tall and usually produced in the 2nd growing season, sparsely puberulent with thin whitish hairs. Leaves dimorphic, the basal leaves to 50 cm long, with long petioles and broad laminae abruptly narrowed at the base, leaves of the stem becoming progressively smaller upward on the stem. Inflorescences (glomerules) subtended by lanceolate leaves on distal stems; perianth parts narrowly oblong to spatulate, often keeled on the back.

An important root and vegetable crop, grown at higher elevations in the tropics. Generally referred to as *Acelga* and *Remolacha*, the species can be divided into two general groups of cultivars:

- Cicla group: Includes the leafy vegetable and ornamental varieties, such as the leaf beet, spinach beet, chard, and Swiss chard. The root is not greatly thickened, the leaves become as much as 25 cm broad and often have a thick midrib. The ornamentals often have reddish leaves.
- Crassa group: Includes those grown for the root, such as the garden beet, red beet, yellow beet, and sugar beet. The root may be short or long, but is thick, from white or yellow to dark wine red.



## CHENOPODIUM Linnaeus

Herbs or subshrubs, annual or perennial, erect or procumbent, often much branched, often with minute scurfy or inflated farinose hairs. Leaves alternate and simple, often larger near the base and becoming progressively smaller on the distal branches, the larger laminae with petioles, laminae entire to pinnatifid, usually gradually narrowed at the base and decurrent on the petiole, gland dots or pale whitish farinose scales often present. Inflorescences basically of small groups of flowers (glomerules) solitary or congested together, axillary or terminal, often subtended by reduced leaves, the axillary or distal flowering stems often spicate or paniculate in form, the flowers lacking both bracts and bracteoles; flowers bisexual or unisexual, radially symmetrical, perianth of (3) 5 parts, free or united near the base, broadly imbricate, white or greenish, drying thin; stamens 3–5, often variable in number on the same plant, filaments short and flat, free or united at the base, anthers introrse, ovary superior and subglobose, style short or none, stigmas 2–5, fimbriate to subulate. Fruit an indehiscent utricle, subglobose to ovoid, the pericarp membranaceous or fleshy, free or adherent to the seed, perianth persisting and loosely enclosing the fruit; seed usually cochleate-lenticular, held vertically (with long axis parallel to the floral axis) or horizontally (with long axis at right angle to the floral axis), embryo coiled into a ring (annular) around the central endosperm.

A chiefly temperate genus with perhaps 100 species, best represented in northern North America. Most species are weedy, and a few are now distributed around the world. Our representatives seem not to be native, and the key includes a species not yet recorded but likely to be introduced. Plants of the genus are sometimes used as green vegetables; the seeds and inflorescences of *C. quinoa* Willd. provide a grain for the Andean people of Ecuador and Peru. Some are used for condiments, and one of our species is used as a vermifuge; see the treatment of this genus in the Flora of Guatemala (Fieldiana, Bot. 24, part 4:139–143, 1946).

- 1a Plants strongly aromatic, with minute yellowish glands on the undersides of leaves, not farinose; seeds black and lustrous, ca. 0.7 mm broad, embryo not completely encircling the endosperm, seeds both vertical and horizontal within a glomerule of flowers; inflorescences paniculate or spikelike, flowers and glomerules mostly sessile; occasional in Costa Rica, 1,000–2,600 m elevation ..... *C. ambrosioides*
- 1b Plants not strongly aromatic, yellowish gland dots absent, with gray or whitish inflated hairs and appearing farinose (as if dusted with flour); seeds more than 1 mm broad, dull or lustrous, horizontal, embryo completely encircling the endosperm; rare or unrecorded in Costa Rica ..... 2a
- 2a Seed with a blunt edge, 1–2 mm in diameter, testa with radial furrows, the pericarp easily removed from the seed; inflorescences to 10 cm long and leafless distally; stems often reddish; a recent introduction ..... *C. album*
- 2b Seed with a sharp edge, 1.2–1.5 mm in diameter, testa surface with rounded pits, pericarp difficult to remove from the seed; inflorescences to 5 cm long, often branched, leafless except at the base; unrecorded from Costa Rica and not included in the descriptions: *C. murale* L.

***Chenopodium album* L., Sp. Pl. 219. 1753.**

Herbs to 1.5 m tall, usually much branched, stems often with longitudinal stripes of pale yellow and green (dry), leafy internodes 0.5–10 cm long, minutely puberulent with crooked whitish hairs but becoming glabrous. Leaves very variable on the same plant with the distal leaves becoming linear-oblong, petioles with thin lateral margins; larger laminae 2–8 cm long, 1–5.5 cm broad, broadly rhombic-ovate to narrowly oblong, margins entire or with up to 10 shallow teeth on each side, upper surface smooth and glabrous, lower surface with minute (0.1 mm) translucent or whitish oblong scales (inflated hairs) and farinose in appearance, venation pinnate or subpalmate with a prominent pair of basal secondaries. Inflorescences of axillary stems with alternate sessile flower clusters and spikelike or with some flower clusters (glomerules) stalked and panicle-like, distal flower clusters without subtending reduced leaves; flowers 1–1.5 mm broad, perianth with farinose scales, ovary with 2 stigmas. Fruit with pericarp easily removed from the seed, seed

1.2–1.6 mm in diameter, circular or slightly ovate in outline, thick-lenticular and with a rounded edge, dull or shiny black.

A weedy species of worldwide distribution, but only recently collected in Costa Rica by J. M. Orozco near Cartago and by J. Gómez-Laurito at Faldas del Irazú; both collections were made in June. The species is recognized by the grayish coloring and scales. In the area near Faldas del Irazú, it is found as a weed in potato fields and is called *Mejicano*.

***Chenopodium ambrosioides* L., Sp. Pl. 219. 1753. *C. anthelminticum* L., Sp. Pl. 220. 1753. Figure 38.**

Herbs, upright or leaning over other plants, 0.1–1.5 (2) m tall, annual or perennial, usually much branched, stems often with longitudinal pale-colored ridges, leafy internodes 0.5–30 mm long, 0.5–4 mm thick, glabrous or very minutely and sparsely puberulent, strongly aromatic with a sharp unpleasant odor. Leaves very variable in size and shape on the same plant, the distal stems with smaller (6–15 mm × 1–4 mm) narrowly oblanceolate laminae, petioles 1–10 mm long, with narrow lateral margins continuous with the laminae margins; larger laminae 2–7 (10) cm long, 1–2.5 (4.5) cm broad, elliptic to obovate in general outline, acute at the apex, gradually narrowed to the base and decurrent on the petiole, margins entire in small laminae but with 2–6 short teeth or lobes on each side of the larger leaves, sometimes pinnatifid, laminae drying thin and chartaceous, smooth and glabrous above, usually glabrous and glandular punctate beneath but the small gland dots often difficult to see on dried material, venation pinnate with 3–6 pairs of secondary veins. Inflorescences spikelike or paniculate, solitary, axillary or terminal, usually made up of an unbranched rachis with clusters (glomerules) of sessile or subsessile flowers often subtended by reduced linear leaves, flowering rachis minutely and sparsely puberulent with thin whitish hairs less than 0.4 mm long; flower buds small and globose or somewhat flattened distally, 0.6–1.5 mm in diameter, bisexual and male flowers found on the same plant, perianth 3- to 5-parted, greenish, rounded; anthers ca. 0.3 mm long, stigmas 3 or 4. Fruit with pericarp easily removed from the seed, seed cochleate-orbicular in outline, lenticular with rounded edges, smooth and lustrous, black.

A weedy species of open early secondary vegetation. Collected only in the highlands (1,000 to 2,600 m) in Costa Rica and probably flowering throughout the year, but with fertile collections made only in January, March, August, and October. This species ranges widely as a weed in both the tropics and subtropics, but may be native to North America.

*Chenopodium ambrosioides* is recognized by its unpleasant odor, alternate leaves that vary from toothed to entire and become smaller and narrower as they progress up the stem, small flowers in small clusters of three to eight often on spikelike stems, and restriction to open weedy habitats. Despite its strong odor, this species is used for flavoring food in Guatemala. The species has been used effectively as a medicinal plant for the removal of intestinal parasites.

### SPINACIA Linnaeus

Herbs, annual, erect, unisexual (dioecious). Leaves alternate, petiolate, laminae usually broadest at the base, often with lobes or teeth on the base and lower half, triangular to hastate, becoming entire and lanceolate distally. Flowers small, rarely bisexual; male flowers in terminal spikes or panicles, perianth 4- or 5-lobed, stamens 4 or 5; female flowers mostly axillary, subtended by 2 bracts which become thick and united in fruit, ovary with 4 or 5 exerted stigmas. Fruit enclosed within the thick united bracts; seed vertical.

A genus of five species, originally from western Asia and growing best in cooler climates. This is the species referred to as *Espinaca* or Spinach in Europe, but these names are also used for *Tetragonia tetragonioides* of the Aizoaceae (q.v.) which grows better in warm climates.

***Spinacea oleracea* L., Sp. Pl. 1027. 1753.**

Herbs to 0.8 m tall, glabrous. Leaves dimorphic, basal and in a rosette or cauline and alternate, laminae broadly ovate and with basal lobes to oblong or narrowly obovate, becoming smaller and narrower up the stem, lanceolate in the distal flowering branches (inflorescences), glabrous, venation pinnate. Fruit enclosed in the thickened carpel-like bracts, occasionally with spines, capsule-like.

**AMARANTHACEAE**

Herbs, shrubs or clambering plants, rarely small trees, bisexual or rarely unisexual, puberulent or glabrous, stems often marked with reddish coloring; stipules absent. Leaves alternate or opposite, petiolate, simple and entire (rarely somewhat crenate or serrate), the lamina often decurrent on the petiole, midvein often extending beyond the lamina as a small mucronate tip, venation usually pinnate. Inflorescences axillary or terminal, solitary or several, the flowers usually borne in congested fascicles or small condensed cymose glomerules and these often arranged in heads or spikes, the flowers usually subtended by a basal bract and 2 lateral bracteoles, these usually stiff and dry and sometimes colorful, glomerules occasionally with sterile flowers modified to aid protection or dispersal. Flowers bisexual or unisexual, generally small and radially symmetrical, sessile or subsessile, perianth (1-3) 4- or 5-parted in 1 or 2 whorls, usually stiff, dry and imbricate, usually narrow, greenish to whitish, pink or reddish; stamens usually as many as the perianth parts and opposite them (rarely 1-3), straight in bud, filaments free or united to form a short or long tube, the tube often with appendages (pseudostaminodia) between the anther-bearing filaments, anthers 2- or 4-theous, medially attached and introrse; ovary superior and 1-locular, 2- or 3-carpellate, with 1 (more rarely several to many) ovules pendulous from long erect funicles from a basal placenta, styles 2 or 3 (1-8), stigmas capitate or filiform. Fruit a 1-seeded utricle or nut, less often a several-seeded capsule or berry, often with circumscissile dehiscence, sometimes indehiscent, the fruit usually included within the persisting bracts, bracteoles, and perianth parts; seed lenticular or reniform, often cochleate-orbicular in outline, often lustrous and smooth, embryo annular or U-shaped, with perisperm.

The Amaranthaceae probably exceed 60 genera and 900 species in number, ranging throughout the tropics and warm temperate areas. They are especially well represented in Africa and the Americas. The family is closely related to the Chenopodiaceae, but that family is often succulent, with the perianth more sepaloid and the filaments bent inward in bud. The Amaranthaceae are usually easy to recognize because of their simple entire estipulate leaves, small flowers, stiff dry grasslike floral bracts and perianth parts, stamens opposite the perianth parts, and basal ovule(s) often producing shiny lenticular seeds with curved embryo. Most of our species are weeds of recently cleared soil or early secondary vegetation. Some species of *Amaranthus*, *Celosia*, *Gomphrena*, and *Iresine* are used in ornamental plantings and in dried flower arrangements because of their colorful, often long-persisting, inflorescences. Several species are used as potherbs, and the grain amaranths (*Amaranthus* spp.) have been an important source of food in some cultures. For a recent review of their use as vegetables, see: Vegetables for the Hot Humid Tropics, Part 6, *Amaranthus* and *Celosia* (1979), available from the Mayagüez Institute of Tropical Agriculture, P.O. Box 70, Mayagüez, Puerto Rico, 00708.

**KEY TO THE GENERA OF AMARANTHACEAE IN COSTA RICA**

- 1a Leaves alternate along the stem; stigmas 2-8; fruit a 1-seeded utricle or capsule or a many-seeded capsule or berry, the fruit loosely enclosed within persisting perianth and bracts ..... 2a
- 1b Leaves opposite along the stem (but sometimes alternate within the inflorescences); stigma 1-3; fruit 1-seeded, usually a thin-walled utricle or indehiscent. .... 5a



- 2a Fruit a many-seeded capsule (or occasionally berry-like); ovary with several to many ovules, stigmas 2–8 and usually exerted beyond the perianth parts; filaments united to form a tube or a shallow cup. . . . . 3a
- 2b Fruit a 1-seeded utricle; ovary with a single basal ovule, stigmas 2 or 3 and exerted or included within the perianth; filaments free or united for ca.  $\frac{1}{3}$  their length to form a cup. . . . . 4a
- 3a Capsule or utricle larger than the perianth parts, the perianth parts often reflexed; seeds usually more than 10, stigmas 2–8 and equal to or longer than the style; inflorescences panicle arrangements of racemes; leaves usually ovate; shrubs of evergreen forest formations. . . . . *Pleuropetalum*
- 3b Capsules or utricles not exceeding the erect persisting perianth parts; seeds usually fewer than 9, stigmas 2 or 3 and shorter than the style; inflorescences spicate (or terminal and broadly flattened or folded and brightly colored in some horticultural forms); leaves usually lanceolate; herbs of open secondary growth or grown in gardens. . . . . *Celosia*
- 4a Erect or prostrate herbs of open secondary vegetation or sometimes cultivated for the colorful inflorescences (densely flowered spikes in terminal panicle arrangements) or for the small edible grains; bracts equal to or larger than the perianth; flowers mostly unisexual, filaments free; seeds 0.5–1.5 mm broad . . . . . *Amaranthus*
- 4b Vining or clambering shrubs of primary and secondary vegetation; bracts much shorter than the perianth parts; flowers bisexual, filaments united at the base, seeds 1.5–2.5 mm broad . . . . . *Chamissoa*
- 5a Inflorescences elongate (5–20 cm) spikes with the fruiting flowers or flower clusters (glomerules) becoming reflexed (pointing backward toward the base) on the spike; fruit tightly enclosed within perianth and bracts, bracts and bracteoles usually with spine tips; anthers 2- or 4-theous, style 1 with a capitate stigma . . . . . 6a
- 5b Inflorescences of short congested spikes or heads or racemes, often in panicle arrangements, flowers or glomerules not strongly reflexed on the inflorescence axis or branches; fruit loosely or tightly enclosed within the bracts and perianth, bracts and bracteoles rarely with spine tips (in *Alternanthera* spp.); anthers 2-theous, styles 1–3, stigmas filiform, cylindrical, or capitate . . . . . 7a
- 6a Spine tips of perianth and bracts straight, not becoming hooked in fruit, flowers solitary and not borne in glomerules or fascicles together with sterile (modified) flowers; perianth parts without prominent ribs; seeds 0.8–1.2 mm broad . . . . . *Achyranthes*
- 6b Spines of some perianth parts and bracts becoming hooked at the apex in late stages, glomerules composed of fertile and sterile flowers; perianth parts with prominent longitudinal ribs abaxially; seeds 1–2.5 mm broad . . . . . *Cyathula*
- 7a Leaves mostly linear and succulent, clasping the stem at their base (amplexicaul) and lacking a well-defined petiole; usually procumbent succulent plants growing at the seashore; filaments united at the base to form a short tube, style with 2 stigmatic branches . . . . . *Philoxerus*
- 7b Leaves neither linear nor succulent, with well-defined petioles and not clasping the stem; plants mostly erect. . . . . 8a
- 8a Inflorescences of spikes in panicle arrangements; flowers unisexual or bisexual, with a conspicuous tuft of whitish hairs developing from under the fruit or from under the fruiting perianth; stigmas 1–3 and filiform . . . . . 9a
- 8b Inflorescences spikes or gloemules, the spikes and glomerules solitary or in few-branched cymes or corymbs; flowers bisexual, a tuft of hairs not produced under flower or fruit in late stages; stigmas 1 or 2 and filiform to capitate . . . . . 10a
- 9a Flowers bisexual, stigma solitary and 2-lobed; outer 3 perianth parts much broader than the inner, basal hairs arising from within (adaxially to) the perianth; clambering shrubs . . . . . *Pfaffia*
- 9b Flowers unisexual or bisexual, stigmas 2 or 3 and filiform to deltoid; perianth parts subequal, basal hairs arising from the outside (abaxial) base of the perianth; erect herbs or clambering shrubs, often common in secondary growth and with conspicuous whitish inflorescences . . . . . *Iresine*
- 10a Stigma 1, capitate or short-cylindric, anthers borne on slender filaments; bracts and bracteoles much shorter than the perianth parts, bracteoles lacking dorsal (abaxial) crests or ridges. . . . . *Alternanthera*



- 10b Stigmas 2 and filiform, anthers sessile on the staminal tube; bracts and bracteoles equaling or exceeding the perianth parts, usually with crenate or serrate crests on the back (abaxially) of the distal half of the bracteoles (in our species). . . . . *Gomphrena*

### ACHYRANTHES Linnaeus

Herbs or subshrubs, annuals or perennials, usually becoming woody at the base, erect or decumbent, puberulent or glabrous; stipules absent. Leaves opposite and simple, petiolate, laminae entire and pinnately veined, usually puberulent. Inflorescence solitary, terminal or axillary, a spike or spikelike raceme, the flowers on very short pedicels and becoming reflexed on the inflorescence, flowers subtended by a bract and 2 bracteoles, the bracts and bracteoles of similar size, often with 1 or 2 stiff straight sharp spines, the bracteoles with the spine far exceeding the thin translucent lobes (in ours), flowers bisexual, essentially radially symmetrical, sepals 4 or 5, free, subequal, narrow and concave, longitudinally ribbed, glabrous or puberulent, becoming stiff and dry, persisting but not enlarging in fruit, stamens usually as many as the perianth parts and opposite them (rarely 2 or 3), united near the base to form a short tube, the tube with pseudostaminodial appendages, anthers 2- or 4-theous, opening introrse, ovary ovoid and often narrowed at the base, 1-locular, the solitary ovule borne from the basal placenta on a long funicle, style and stigma 1. Fruit an indehiscent utricle (or like an achene when the fruit wall is stiff), tightly enclosed by bracts and perianth, usually reflexed and appressed against the axis of the inflorescence; seeds somewhat flattened, the embryo curved.

A weedy genus of probably five to 10 species with two species now widely naturalized in the neotropics. The genus is thought to have been confined to the Old World until recently. These plants are characterized by the opposite leaves, long spikelike inflorescences with flowers and fruit becoming reflexed and appressed on the rachis, the bracts with stiff straight spines, and the utricles tightly enclosed within perianth and bracts.

- 1a Larger laminae ovate to elliptic and with acuminate apices; sepals 5–7 mm long; 0–1,200 m . . . . . *A. aspera*  
 1b Larger laminae broadly obovate to obovate-orbicular, abruptly rounded or truncated at the apex; sepals ca. 4 mm long; 0–400 m . . . . . *A. indica*

***Achyranthes aspera* L., Sp. Pl. 204. 1753. *Centrostachys aspera* (L.) Standl., J. Wash. Acad. Sci. 5:75. 1915. Figure 25.**

Herbs or subshrubs, 0.4–1.5 (2) m tall, woody in the lower parts and usually erect, leafy internodes (1) 2–15 cm long, 2–5 mm thick, puberulent with whitish ascending sericeous hairs ca. 1 mm long, longitudinally striate and brown when dry, usually terete. Leaves opposite and decussate, often quite variable on the same plant, petioles 3–30 (40) mm long, densely sericeous, with lateral margins forming an adaxial sulcus near the base and continuous with the lamina margins distally; laminae 2–18 (25) cm long, 1–8 (10) cm broad, ovate to elliptic or slightly obovate, apically obtuse on the smaller leaves but acuminate on the larger leaves, obtuse to attenuate at the base, margin entire or obscurely crenate (dried) and decurrent on the petiole, the laminae drying thin- to stiff-chartaceous, smooth on both surfaces, sparsely to densely sericeous to strigillose with the lower surface more densely puberulent than the upper, with 3–7 pairs of major secondary veins arising at angles of 40°–60°. Inflorescence usually solitary and terminal, spikes 10–40 cm long, 6–14 mm broad, the flowers at first closely crowded and divergent but soon becoming separate and reflexed, bracts and bracteoles with 1 or 2 sharp stiff spines, 2–4 mm long, pedicels 0.1–0.5 mm long; flowers essentially subsessile and becoming reflexed on the spike, sepals 5–7 mm long, lanceolate, very stiff. Fruit enclosed by the tightly appressed bracts and perianth, reflexed and appressed against the axis of the spike, utricle ca. 3 mm long and 1 mm thick, cylindrical with a truncated apex and rounded base, difficult to separate from the enclosing perianth.

Plants of open weedy sites and early successional stages from sea level to about 1,200 m elevation in both evergreen and seasonally very dry deciduous areas;

flowering and fruiting collections have been made from November to April in our area. The species appears to be an introduction from the Old World.

*Achyranthes aspera* is recognized by the long slender spikes with retrorse flowers and fruits enclosed in spine-bearing bracts and stiff perianth parts, the thin acuminate leaves, and open-branched growth habit. The larger leaves with acute or acuminate apices and the perianth parts always 5 mm long or more are consistent traits that distinguish this species from *A. indica* in our area. The spines on the bracts and bracteoles are an effective aid in dispersal. The plants are called *Rabo de Chancho*, *Mosotillo*, and *Mozote*.

***Achyranthes indica* (L.) Miller, Gard. Dict. ed. 8, no. 2. 1768. *A. aspera*  $\beta$  *indica* L., Sp. Pl. 204. 1753. *Centrostachys indica* (L.) Standl., J. Wash. Acad. Sci. 5:75. 1915. Figure 25.**

Herbs or subshrubs, to 1 m tall (rarely taller), woody at the base, leafy internodes (1) 3–15 cm long, 1–4 mm thick, puberulent with thin whitish ascending hairs 0.2–1 mm long, grayish and longitudinally striate when dry, terete or angular. Leaves opposite and decussate, petioles 1–8 (15) mm long, poorly differentiated from the lamina, with lateral margins continuous with the lamina margins, densely sericeous; laminae 1.5–6 (8) cm long, 1–4 cm broad, broadly obovate to obovate-orbicular or rhombic-orbicular (broadly elliptic in small leaves), rounded or abruptly obtuse at the apex with a small acute tip, usually cuneate at the base, margin entire and decurrent on the petiole, the laminae drying thin- to stiff-chartaceous, smooth to the touch and puberulent on both surfaces, densely sericeous beneath with thin ascending whitish hairs ca. 0.3 mm long, with 5–8 pairs of major secondary veins. Inflorescences terminal (often terminal on short axillary shoots), 10–30 cm long, 5–10 mm broad, axis of the spike with spreading thin whitish hairs, flowers at first crowded and divergent but soon becoming separate and reflexed, bracts and bracteoles with stiff spines 2–3 mm long; flowers subsessile, perianth parts ca. 4 mm long, lanceolate, pale green, tightly enclosing the fruit. Fruit tightly enclosed within the spinose bracts and the stiff dry perianth parts, reflexed on the flowering axis, utricle somewhat cylindrical, ca. 2 mm long and 1 mm thick, difficult to separate from the enclosing perianth.

Plants of open bare soils and early successional vegetation below 400 m elevation in both evergreen and seasonally very dry deciduous formations in Central America; probably flowering throughout the year, but with collections in our area only from December through March, July, and August. The species is probably an introduction from the Old World.

*Achyranthes indica* is recognized by its long slender spikes with retrorse flowers and fruits tightly enclosed in spine-bearing bracts and stiff dry perianth parts, puberulent leaves with blunt rounded apices, and short stature in open or recently disturbed sites. The bluntly rounded leaves and shorter perianth parts consistently distinguish these plants from *A. aspera* in our area. The two taxa were treated as varieties in the Flora of Panama (Ann. Missouri Bot. Gard. 48:24, 1961), but they seem to behave like two different species in Central America.

#### ALTERNANTHERA Forsskål

Herbs or small subshrubs, annuals or perennials, prostrate, erect or clambering, bisexual, usually puberulent in early stages. Leaves opposite, petioles present, poorly differentiated or absent; laminae simple and essentially entire, puberulent or glabrous, venation pinnate. Inflorescences axillary or terminal, 1–3 at a node, sessile or pedunculate, capitate or spicate, each flower usually with a subtending bract and 2 lateral bracteoles, the bracts and bracteoles similar or differing in size and shape. Flowers bisexual, radially symmetrical, sessile or subsessile, perianth 5-parted, the perianth parts free with the inner and outer whorls similar or differing in size and form, usually concave, dry and stiff, ovate to



FIG. 25. Amaranthaceae: Costa Rican representatives of *Achyranthes* and *Cyathula*. Note the hooked hairs of *Cyathula*.

lanceolate and usually acute at the apex, longitudinal ribs often thickened on the abaxial side, whitish to purple or pale yellowish, persisting but not enlarging in fruit; stamens 3–5, united in the lower part to form a tube, usually with staminode-like projections on the tube between the anther-bearing filaments, anthers oblong and 2-theous, introrse; ovary superior and globose to ovoid or obovoid, usually laterally flattened, 1-locular with 1 ovule borne on an elongate funicle from a basal placenta, style short or long, stigma solitary. Fruit a thin-walled utricle, indehiscent, tightly or loosely enclosed within the persisting perianth; seeds cochleate-reniform to orbicular or ellipsoid in outline, usually lenticular in cross section, smooth and lustrous, embryo annular.

A genus of perhaps 100 species best represented in the Neotropics, but with many species now widely ranging as weeds in tropical and subtropical to warm-temperate areas. Our species are distinguished by their small whitish heads (except in *A. costaricensis*), densely crowded little flowers subtended by usually similar bracts and bracteoles, longitudinal ribs on the back of the outer perianth parts often thickened, both bracts and perianth parts often terminating in sharp spinelike tips, and preference for open early secondary growth habitats (except in *A. costaricensis*). This genus is very similar to *Gomphrena* (q.v.), and the nomenclature of the two genera has been badly confused (see J. A. Mears in Proc. Acad. Nat. Sci. Philadelphia 129:1–21, 1977, and in Taxon 29:85–95, 1980). This treatment is based on the annotations and identifications of our material by James Mears.

- 1a Inflorescences pedunculate, not subtended by leaves; internodes often more than 5 cm long, leaves usually 4–14 cm long, plants usually erect; seeds lustrous black . . . . . 2a
- 1b Inflorescences sessile in the axils of leaves, less than 12 mm long (except in *A. costaricensis*); plants erect, clambering or prostrate; seeds lustrous brown or reddish brown . . . . . 5a
- 2a Perianth parts sparsely puberulent or glabrous, inflorescences rarely more than 1 cm long, floral bracts 1–1.5 mm long and often with a sharp tip; 1,000–2,200 m altitude. . . . . *A. lanceolata*
- 2b Perianth parts densely puberulent or ciliate, inflorescences often more than 1 cm long, floral bracts more than 2 mm long . . . . . 3a
- 3a Floral bracts 4–6 mm long with an erose or ciliate margin and often with very short (0.5 mm) stiff white hairs; seed ellipsoid, ca. 1.8 mm long; 0–1,000 m but rarely collected in southern Central America . . . . . *A. brasiliana*
- 3b Floral bracts 2–4 mm long, with an entire margin; 0–1,500 m . . . . . 4a
- 4a Perianth with long (4 mm) thin whitish hairs; seeds ca. 0.7 mm long; leaves lanceolate to very narrowly elliptic; common in Costa Rica in wet evergreen formations . . . . . *A. laguroides*
- 4b Perianth with short (0.5 mm) hairs; seeds ca. 1.5 mm long; leaves elliptic to elliptic-ovate; rare in Costa Rica and usually found in seasonally deciduous areas . . . . . *A. pubiflora*
- 5a Plants usually prostrate, laminae rarely exceeding 2.5 cm in length; plants rarely collected in Costa Rica; fruit truncated at the apex and with the style usually persisting . . . . . 6a
- 5b Plants erect, clambering, or occasionally forming low mats; laminae often exceeding 2.5 cm in length; fruit rounded or emarginate (notched) at the apex . . . . . 7a
- 6a Perianth with thin hairs minutely hooked ( $\times 25$ ) at the ends; fruit tightly enclosed within the persisting perianth; floral bracts ca. 3 mm long . . . . . *A. caracasana*
- 6b Perianth with thin white hairs lacking very minute hooks at the tip; fruit easily removed from the persisting perianth; floral bracts 1–2 mm long . . . . . *A. paronychioides*
- 7a Plants erect or clambering on others and forming mats; often found in open sunny early secondary sites, common wild plants in evergreen and partly deciduous areas . . . . . 8a



- 7b Plants erect; found in gardens or in deep forest shade ..... 9a  
 8a Laminae to 9 cm long and 4 cm broad; floral bracts 2 mm long, perianth ca. 4 mm long; fruit tightly enclosed within the persisting perianth; suborbicular ..... *A. tenella*  
 8b Laminae to 6.5 cm long and 2 cm broad; floral bracts 0.5–1 mm long, perianth ca. 2 mm long; fruit loosely enclosed by the perianth, lenticular, notched at the apex ..... *A. sessilis*  
 9a Laminae 7–16 cm long; inflorescences 1–4 cm long and drying brownish, perianth parts to 8 mm long; rarely collected plants of wet forest interiors below 1,000 m elevation ..... *A. costaricensis*  
 9b Laminae to 6 cm long, often purplish or marked with varied colors; inflorescences less than 1 cm long, perianth parts ca. 3 mm long; common ornamental plants of parks and gardens ..... *A. bettzichiana*

***Alternanthera bettzichiana*** (Regel) Voss, in Steb. & Voss, *Vilmorin's Blumengärtnerei* 869. 1896. *Telanthera bettzichiana* Regel, *Gartenfl.* 11:178. 1862. *Achyranthes bettzickiana* (Regel) Standl., *N. Amer. Fl.* 21:138. 1918. *Alternanthera bettzickiana* (Regel) Standl., *Publ. Field Columbian Mus., Bot. Ser.* 3:254. 1930. Figure 26.

Cultivated herbs or subshrubs of small (20–80 cm) stature, with many lateral branches and bushlike in form, leafy internodes 0.5–4 cm long, 0.7–3 mm thick (dry), becoming sparsely puberulent, ridged or longitudinally sulcate on drying but succulent in life, with tufts of thin whitish hairs in the leaf axils. Leaves opposite, often with reddish or purple coloring, petioles poorly differentiated from the lamina, 6–25 mm long, ca. 0.5 mm thick when dry, with lateral margins continuous with the lamina margins; laminae 0.5–4 cm long, 0.5–2 cm broad, obovate to oblanceolate, obtuse at the apex, gradually narrowed at the base and decurrent on the petiole, margins entire, the laminae drying stiffly chartaceous, sparsely puberulent or glabrous, with 2–4 pairs of major secondary veins. Inflorescences solitary and axillary, capitate, 4–8 mm long, floral bracts 1–2 mm long, stiff and with a thickened midrib extending to form a sharp tip; flowers with the outer perianth parts ca. 3 mm long, with 3 longitudinal ribs thickened abaxially, sharply acute at the apex, with thin whitish hairs on the back. Fruit suborbicular, 1–1.5 mm long; seeds 0.8–1.2 mm broad, cochleate-orbicular, lenticular in cross section, shiny reddish brown.

Widely cultivated and perhaps occasionally escaping plants of open sunny sites; to be expected between sea level and about 2,000 m altitude. This taxon may be unknown as a truly wild plant; it is commonly cultivated from the southern United States to Brazil and Peru in the New World and in many areas of the Old World.

*Alternanthera bettzichiana* is distinguished by its variably colored foliage (from reddish and purplish to green marked with yellow or white), short succulent bush habit, small sessile axillary whitish heads, and general restriction to gardens and cultivated plantings. The dense branching and variously colored foliage make these plants especially suitable for planting in rows or dense groups to achieve masses of color in formal gardens and parks. These plants have been called *Colchón de niño* in Honduras, *Coqueta* in Belize, *Monte negro* in Nicaragua, and *Perico* in El Salvador. This species is closely related to *A. tenella* Colla.

***Alternanthera brasiliana*** (L.) O. Kuntze, *Rev. Gen.* 1:537, 1891. *Gomphrena brasiliana* L., *Cent. Pl.* 2:13. 1756. *Achyranthes brasiliana* (L.) Standl., *J. Wash. Acad. Sci.* 5:74. 1915.

Herbs, annual or perennial, erect or prostrate, leafy internodes 3–10 (18) cm long, 0.7–3 mm thick, strigose with thin white ascending hairs 0.5–2 mm long. Leaves opposite, petioles 3–10 mm long, with narrow lateral margins continuous with the lamina margins;

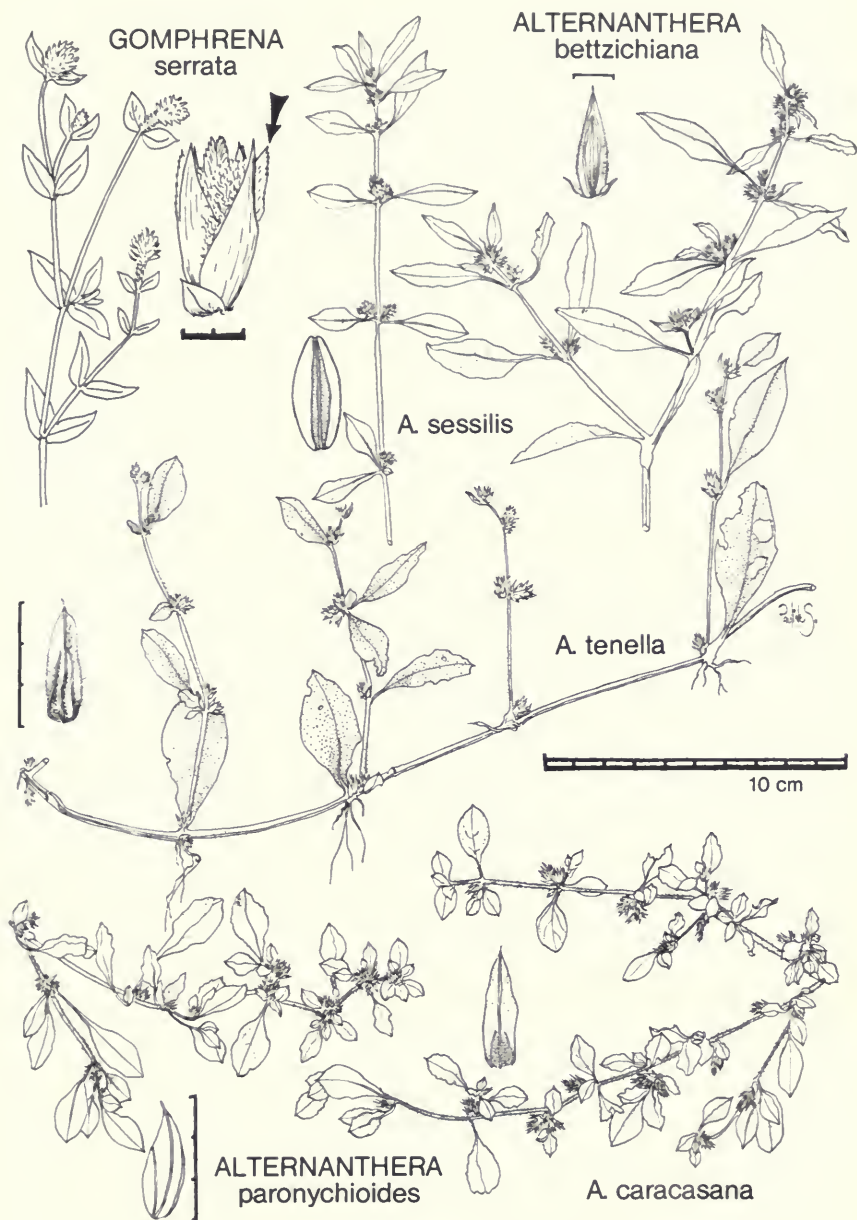


FIG. 26. Amaranthaceae: species of *Alternanthera* with sessile inflorescences and a common species of *Gomphrena*. The arrow denotes the dorsal crest on the floral bract of *Gomphrena serrata*.

laminae 2–10 cm long, 1–6 cm broad, elliptic to ovate-elliptic or lanceolate, tapering gradually or abruptly to the acute or short-acuminate apex, rounded to obtuse at the base and decurrent on the petiole, margins entire, the laminae drying thin-chartaceous, puberulent on both surfaces with whitish appressed-ascending hairs 0.2–1.5 mm long, venation pinnate with 3–6 pairs of major secondary veins. Inflorescences solitary, usually terminal, compact spikes or capitula 10–20 mm long and 8–14 mm thick, white or yellowish, borne on slender peduncles 2–16 cm long, with slender ascending stiff hairs, floral bracts 4–6 mm long, the distal margin erose or ciliate, midrib obscure, glabrous or minutely puberulent; flowers sessile or subsessile, perianth parts 3–6 mm long and often obscured by the bracts and bracteoles, ovate-lanceolate, with 3 longitudinal ribs prominent on the basal half, stamens and pistil hidden within the persisting perianth and bracts. Fruit included within the persisting perianth and bracts; seed ellipsoid, ca. 1.8 mm long, lustrous black.

Herbs of open sunny sites often in sandy soils below 1,000 m elevation and flowering throughout the year. Known from a single collection in Nicaragua and to be expected in Costa Rica; the species is native to Venezuela, the Guianas, Brazil, and eastern lowland Peru.

*Alternanthera brasiliensis* is recognized by the opposite leaves with conspicuous hairs, long internodes, terminal and solitary white or yellowish heads on long peduncles, and large floral bracts. The species has recently been collected near Esteli in Nicaragua (*Molina* 23058), but it has not been recorded from Costa Rica or Panama.

***Alternanthera caracasana* H.B.K., Nov. Gen. & Sp. 2:206. 1818. Figure 26.**

Densely branched usually prostrate herbs, 5–25 cm tall, leafy internodes 0–4 cm long, 0.7–2 mm thick (dry), densely sericeous or villous with thin whitish hairs 1–2 mm long. Leaves opposite and small, often clustered at the nodes, petioles 1–5 mm long, with lateral margins continuous with the lamina margins; laminae 0.5–2 cm long, 3–12 mm broad, elliptic to obovate, abruptly obtuse or rounded at the apex, gradually narrowed to the attenuate base, margins entire, the laminae drying chartaceous, sparsely puberulent, venation often obscure, with 1–3 pairs of secondary veins. Inflorescences solitary and sessile in the axils of leaves, short spikes 5–10 mm long, floral bracts ca. 3 mm long, the prominent midvein short-cuspidate at the apex, broadly ovate and thin-translucent, mostly glabrous; flowers tightly clustered, outer perianth parts ca. 3 mm long, often obscured by the bracts, the midrib prominent and often extended to form a short (1 mm) apical spine, 2 lateral longitudinal ribs often thickened near the base, puberulent on the back (abaxially) with thin whitish hairs that are minutely hooked at the tip. Fruit tightly enclosed within the persisting perianth; 1.5–2 mm long, truncate at the apex and with a persisting style; seeds ca. 1.5 mm long, cochleate-ovoid, lenticular in cross section, lustrous brown.

Prostrate plants of open early secondary habitats, known only as weeds near large urban centers in Costa Rica between 1,000 and 1,500 m elevation. The species flowers throughout the year in northern Central America and ranges from about 500 to 2,500 m elevation (rarely collected below 500 m in Guatemala). The species ranges from Mexico (in both low and higher altitudes) through Central America and the West Indies to northern and western South America as far as Bolivia.

*Alternanthera caracasana* is recognized by its prostrate habit, small leaves and small sessile inflorescences, and by the unusual "grappling hook" hairs on the back of the outer perianth parts. These small hairs have very minute terminal hooks that are quite difficult to see with a 10× hand lens and are sometimes interspersed with hairs lacking the hooks. Most of our Central American material of this species was previously placed under the name *A. repens* (L.) Kuntze. The species appears to be quite rare in Costa Rica.

***Alternanthera costaricensis*** O. Kuntze, Rev. Gen. 2:538. 1891. *Achyranthes costaricensis* (Ktze.) Standl., J. Wash. Acad. Sci. 5:74. 1915. *Achyranthes megaphylla* Standl., North Amer. Fl. 21:141. 1917, ex char. Figure 27.

Herbs or subshrubs 20–80 cm tall, apparently perennial, erect and usually unbranched, leafy internodes 1–9 cm long, 1–3.5 mm thick, with thin usually straight appressed-ascending yellowish hairs 0.5–1 mm long, stems becoming dark brown and glabrous. Leaves opposite, petioles 5–10 mm long, puberulent with appressed-ascending hairs, usually becoming glabrous; laminae 7–16 (17.5) cm long, 2–5 (7.5) cm broad, narrowly elliptic to narrowly ovate-elliptic or ovate-oblong, tapering gradually to a sharply acuminate or acute apex, acute to obtuse at the base, margins entire, the laminae drying thin-chartaceous, smooth above and below, with scattered thin straight ascending hairs above and (more densely) below, the 7–10 pairs of major secondary veins arising at angles of 50°–70°. Inflorescences sessile or subsessile in the axils of terminal or distal leaves, solitary and spicate, 1–4 cm long, ca. 1 cm thick, greenish in life but drying yellowish brown or brown, floral bracts 3–4 mm long, ovate but narrowed to a sharp tip ca. 1 mm long, with a single midrib, rachis visible between the flowers and bracts, densely pilose; flowers with the outer perianth parts 6–8 mm long, with 3 or 5 prominent longitudinal ribs, tapering gradually to the sharply acute apex, puberulent at the base. Fruit and seed not seen.

Rare plants in the understory of wet evergreen forests and known only from near sea level to 1,100 m altitude on the Caribbean slopes and lowlands; flowering collections have been made between late March and November. The species has not been found outside Costa Rica and is presently known from as far north as Bijagua (Alajuela) and as far south as Siquirres (Limon).

*Alternanthera costaricensis* stands apart from all our other species of *Alternanthera* because of the elongate inflorescences with very stiff, relatively large, dull brownish perianth parts, deep forest habitat, and relatively large thin leaves. The inflorescences give the impression that this species may be more naturally situated in another genus. The original description of Kuntze states that the spikes are borne on peduncles and, indeed, Kuntze's collection from eastern Costa Rica (NY) gives this impression. However, on closer inspection, the "peduncles" appear to be terminal internodes, with the distal leaves having fallen off. *Note added in proof*: Specimens of this species returned to Field Museum in September 1982 have been annotated *Jamesbondia costaricensis* (Ktze.) Mears by Mears.

***Alternanthera laguroides*** (Standl.) Standley, in Standl. & Calderon, Lista Pl. Salvador. 74. 1925. *Achyranthes laguroides* Standl., Contr. U.S. Natl. Herb 18:90. 1916. Figure 27.

Herbs or subshrubs, erect or clambering, to over 2 m high or 3 m long, older nodes slightly thickened, leafy internodes 5–15 (20) cm long, 0.5–4 mm thick, at first densely sericeous with thin ascending whitish hairs ca. 1 mm long but soon becoming glabrescent, older stems longitudinally striate. Leaves opposite, petioles 1–4 (6) mm long, slightly expanded at the base and with tufts of hairs in the axils; laminae (2) 4–11 (14) cm long, (0.4) 1–2.5 (3.5) cm broad, lanceolate to narrowly elliptic or very narrowly elliptic-oblong, acute at the apex and with a slender sharp tip 1–2 mm long, acute at the base and decurrent on the petiole, margins entire, smooth and sericeous on both surfaces with thin appressed-ascending whitish hairs ca. 1 mm long, the 3–6 pairs of major secondary veins arising at angles of 30°–50°. Inflorescences compact heads or short spikes 4–14 mm (20) mm long, borne on simple (rarely branched) peduncles 1–4 cm long, solitary or 3 together, axillary or terminal, leaves subtending the inflorescences sometimes reduced and the terminal stems and spikes producing panicle-like arrangement, floral bracts 2–4 mm long, with a single midrib and acute tip; flowers sessile, perianth 4–5 mm long, with long (4 mm) thin whitish hairs from the base of the perianth, each perianth part with only a single promi-





FIG. 27. Amaranthaceae: three species of *Alternanthera* and a species of *Pfaffia*.

nent longitudinal midrib, stamens and pistil hidden within the perianth. Fruit hidden within the persisting perianth and bracts; seeds ca. 0.7 mm broad.

Plants of moist evergreen forest formations on both the Caribbean and Pacific sides of Costa Rica from sea level to 1,500 m elevation; flowering collections have been made from January to June. The species, as presently known, ranges from central Nicaragua to central Panama.

*Alternanthera laguroides* is distinguished by its clambering habit, long internodes, pedunculate heads or short spikes, and the relatively long straight whitish hairs borne from the base of the outer perianth parts (abaxially). The plants have been called *Botoncillo* in our area. The species is well represented by collections from Costa Rica, but only a very few *A. laguroides* are from Nicaragua and Panama.

***Alternanthera lanceolata*** (Benth.) Schinz, in Engler & Prantl., *Naturl. Pflanzenfam.* ed. 2, 16C:75. 1934. *Brandesia lanceolata* Benth., *Pl. Hartweg.* 247. 1846. *Alternanthera lehmannii* Hieron., *Bot. Jahrb. Syst.* 20, beih. 49:8. 1895. *Achyranthes lehmannii* (Hieron.) Standl., *J. Wash. Acad. Sci.* 5:74. 1915. *Achyranthes panamensis* Standl., *Contr. U.S. Natl. Herb.* 18:89. 1916. *Achyranthes stenophylla* Standl., loc. cit. 18:90. 1916. *Alternanthera panamensis* (Standl.) Standl., *Publ. Field Columbian Mus., Bot. Ser.* 8:9. 1930. *Alternanthera stenophylla* (Standl.) Standl., loc. cit.

Herbs, 0.3–1 m tall, erect or decumbent, leafy internodes (0.5) 3–15 cm long, 0.7–3 mm thick, at first densely puberulent with thin ascending hairs 0.5–1 mm long but soon becoming glabrescent. Leaves opposite, petioles 2–10 mm long, slender and with very narrow lateral ridges continuous with the laminae margins; laminae 2–8 (15) cm long, 0.5–3 (5) cm broad, elliptic to elliptic-ovate, gradually narrowed to the acuminate apex, acute to obtuse and somewhat decurrent at the base, margin entire, the laminae drying thin chartaceous, sparsely puberulent with thin hairs 0.5–1.8 mm long on both surfaces, with 4–6 pairs of major secondary veins. Inflorescences capitate or very short spikes, 3–10 mm long, solitary or rarely 2–3 on slender (0.3 mm) peduncles (0.5) 2–10 cm long, terminal or axillary, sparsely puberulent, floral bracts 0.5–2 mm long, cuspidate, with broad thin translucent margins; flowers 3–4 mm long, subsessile or sessile, perianth parts ca. 3 mm long, glabrous or very sparsely puberulent, with 3 weakly defined longitudinal ribs, stamens and pistil included within the persisting perianth. Fruit tightly enclosed within the persisting perianth, the seeds 1.2–1.5 mm broad, reniform-rounded, lustrous black, smooth or wrinkled when dry.

Weedy herbs of open and shaded sites in moist and wet evergreen forest formations from 1,000 m to about 2,200 m elevation in Costa Rica; collected with inflorescences from August through January. The species occasionally forms a ground cover along stream and brook beds and appears to be restricted to areas subjected to the very wet Caribbean winds between San Ramon and the Rio Grande de Orosí drainage in Costa Rica; the species ranges from Guatemala to Colombia.

*Alternanthera lanceolata* is recognized by the long slender internodes, usually solitary capitate inflorescences on long peduncles, long hairs on the upper leaf surfaces, perianth parts with weakly developed ribs, and the restriction to cloud forest habitats between 1,000 and 2,200 m (in Costa Rica).

***Alternanthera paronychioides*** St. Hil., *Voy. Brasil*, 2 (2):43. 1833. *Gomphrena ficoidea* L., *Sp. Pl.* 1:225. 1753, non *A. ficoidea* Beauv. 1818. Figure 26.

Herbs, usually prostrate, stems much branched, up to 1 m long and often rooting from the nodes, leafy internodes 1–5 cm long, 0.5–2 mm thick (dry), at first densely sericeous-tomentulose but soon becoming glabrous. Leaves opposite, occasionally somewhat dimorphic in size, petioles 1–15 mm long, with lateral margins continuous with the lamina

margins; laminae 0.6–3 cm long, 0.5–1.5 cm broad, obovate to elliptic, abruptly obtuse to rounded at the apex, gradually narrowed to the attenuate base and decurrent on the petiole margins, entire, the laminae drying thin-chartaceous, very sparsely puberulent, with 2 or 3 pairs of major secondary veins. Inflorescences solitary and sessile in the axils of leaves, capitate or short spikes 4–10 mm long, white, floral bracts 1–2 mm long, thin, obtuse to acute at the apex, with a single thickened midrib; flowers with the outer perianth parts 3–4 mm long, 3 longitudinal ribs prominent on the lower half of the abaxial side, acute and entire, with thin white hairs, anthers 5. Fruit loosely enclosed in the persistent perianth, obovoid and usually truncate at the apex with the base of the style persisting, 1.2–1.8 mm long and equally broad or broader; seeds 0.8–1.2 mm broad, cochleate-orbicular, lenticular in cross section, dark brown and lustrous.

Prostrate weeds of open, usually damp, sites from near sea level to about 1,500 m elevation; probably flowering throughout the year, but most often collected in the wet season. The species ranges from northern Mexico to southern South America. These plants are often found near the seashore and brackish (salty) water.

*Alternanthera paronychioides* is distinguished by its prostrate habit, profuse branching, small sparsely puberulent leaves, small sessile inflorescences, and fruit easily removed from the persisting perianth and bracts. This species appears to be quite rare in southern Central America; I have seen only a single specimen from Costa Rica: *Maxon & Harvey* 8750 from near Puntarenas, close to sea level. While very similar to *Alternanthera caracasana*, this species lacks the unusual grappling-hook hairs (20×) on the back of the outer perianth parts, and the fruit is not tightly enclosed within the fruiting inflorescence. Standley reported *Golondrina* as a common name for this species in Costa Rica, but this species is quite rare and the name may be misapplied here. Central American specimens of this species have often been placed under the name *A. polygonoides* (L.) R. Br. (as in the Flora of Guatemala, Flora of Panama, and Flora of Costa Rica), but Mears considers the Linnaean basonym a nomen obscurum.

***Alternanthera pubiflora*** (Benth.) O. Kuntze, Rev. Gen. 2:538. 1891. *Brandesia pubiflora* Bentham, Bot. Voy. Sulph. 157. 1846. *Achyranthes williamsii* Standley, Contr. U.S. Natl. Herb. 18:89. 1916. *Alernanthera williamsii* (Standl.) Standley, J. Wash. Acad. Sci. 15:458. 1925. Figure 27.

Herbs, erect, procumbent, or clambering, 0.5–1.5 (2) m tall, leafy internodes 2–11 cm long, 0.8–5 mm thick, densely strigilose with small (0.2–0.8 mm) whitish ascending or appressed hairs, becoming glabrescent with age. Leaves opposite, petioles 2–10 (14) mm long, the lateral edges continuous with the lamina margins; laminae 4–12 cm long, 1.5–4 (5) cm broad, elliptic to elliptic-ovate, acute to short acuminate at the apex, gradually narrowed to the obtuse or acute base and decurrent on the petiole, margins entire, the laminae drying thin to stiffly chartaceous, smooth and with thin whitish hairs ca. 0.5 mm long on both surfaces, venation pinnate with 3–6 pairs of major secondary veins. Inflorescences short spikes or capitate, 6–15 mm long, 1–3 borne in the leaf axils or terminal, peduncles slender and sericeous, (0.5) 1–8 cm long, floral bracts 2–3 mm long, ovate-lanceolate, acute at the apex and with a single midrib, bracteoles often with the midrib prolonged and caudate; translucent white, flowers sessile, perianth parts ca. 6 mm long, with 3 prominent longitudinal ribs, and stiff little white hairs on the back (abaxially), stamens and pistil included within the perianth. Fruit enclosed within the persisting bracts, bracteoles and perianth; seed ca. 1.5 mm long, reniform-oblong, lustrous black.

Weedy plants of open and partly shaded sites in the seasonally dry and deciduous or partly deciduous formations between sea level and 800 (1,400) m elevation along the Pacific slope in southern Central America and collected in flower and



fruit from December to June. The species ranges from Nicaragua and primarily along the Pacific slope in South America to Chile, Bolivia, and Argentina.

*Alternanthera pubiflora* is recognized by its larger elliptic leaves, sericeous pubescence on many parts, 3-ribbed perianth parts, smaller bracts and bracteoles, and long-peduncled inflorescences that arise either from the leaf axils or are terminal. The terminal inflorescences are sometimes followed by paired axillary shoots that produce dichotomous branching. While collected quite often in Nicaragua, this species is apparently rare in Costa Rica.

***Alternanthera sessilis* (L.) R. Br., Prodr. 417. 1810. *Gomphrena sessile* L., Sp. Pl. ed. 2, 300. 1762. Figure 26.**

Small herbs, erect or decumbent, 10–50 cm tall and to 1 m long, stems usually with only a few lateral branches, leafy internodes (0.5) 1–8 cm long, 0.5–3 mm thick, very sparsely puberulent with minute crooked hairs usually confined to 2 narrow longitudinal depressions on opposite sides of the stem, leaf axils often with longer (0.5 mm) whitish hairs, an interpetiolar ridge usually joining the leaf bases. Leaves opposite, petioles poorly differentiated from the laminae, 0–5 mm long, with lateral margins continuous with the lamina margins; laminae (1) 1.4–6.5 cm long, 4–14 (20) mm broad, very narrowly elliptic to oblanceolate, bluntly acute (obtuse) at the apex, tapering gradually to the base and decurrent on the petiole, margins entire, the laminae drying thin-chartaceous and usually greenish, smooth and glabrous above and below or with a few minute hairs along the midvein, with 3–6 pairs of major secondary veins. Inflorescences solitary and sessile or subsessile in the axils of leaves, capitate, 3–5 mm long, whitish or slightly pink, floral bracts less than 1 mm long, broadly triangular, thin translucent; flowers sessile, outer perianth parts ca. 2 mm long, thin translucent and with only the midrib thickened. Fruit a utricle 1.5–2 mm long and not tightly enclosed by the persisting perianth, pale yellowish brown, emarginate at the apex and broadly obovate in outline with the style sessile in the apical notch, lenticular in cross section; seeds ca. 1 mm long, pale brown.

Pioneer weeds in open sites, often in wet depressions and river margins, occasionally growing partly submerged in water, from near sea level to 1,200 m elevation in our area; flowering throughout the year, but collected most often from February to August in Costa Rica. The species appears to be uncommon in the seasonally very dry areas of Guanacaste. A pantropical species, ranging from Guatemala and Belize through Central America and the West Indies to Peru and Brazil in the New World.

*Alternanthera sessilis* is distinguished by its small white sessile inflorescences, unusual fruit that is usually visible within the persisting perianth, the laminae tapering gradually to the petiole, and the usually wet habitats. The unusual fruit and the ease with which it can be removed from the dry flowers set this species well apart from its congeners in Central America.

***Alternanthera tenella* Colla, Mem. Reale Accad. Sci. Torino 33:131. 1829. Figure 26.**

Herbs, erect or clambering over other small vegetation, stems to 1 m long, leafy internodes 1–10 cm long, 0.8–3 mm thick, densely puberulent at first with thin or basally thickened whitish hairs ca. 0.5 mm long, soon becoming glabrous, often with tufts of hairs in the leaf axils, the hairs often barbed near the base. Leaves opposite, petioles 1–8 mm long, with lateral margins continuous with the laminae margins; laminae (1.5) 2–9 cm long, (0.5) 1–4 cm broad, elliptic to ovate-elliptic, obtuse to bluntly acute at the apex, tapering gradually to the obtuse or acute base and decurrent on the petiole, margin entire, laminae drying thin-chartaceous, smooth, becoming glabrous or with a few small (0.1–0.5 mm) hairs along the midvein, with 3–6 pairs of major secondary veins. Inflorescences



solitary and sessile in the axils of leaves, capitate or very short spikes 4–10 mm long, 3–6 mm in diameter, whitish, floral bracts ca. 2 mm long, with a sharp aristate tip and translucent margins; flowers sessile, outer perianth parts ca. 4 mm long, stiff and with a sharp tip, with 3 (5) strongly raised longitudinal ridges on the back and short (0.1–0.5 mm) stiff hairs near the base, the hairs occasionally minutely hooked. Fruit a suborbicular utricle tightly enclosed within the persisting perianth, seed cochleate-oblongoid, 1 mm long, lustrous dark reddish brown.

Plants of open sunny early secondary growth, from near sea level to about 500 m elevation in both moist evergreen and in seasonally deciduous areas (but apparently very rare in seasonally very dry Guanacaste); flowering throughout the year in our area, but collected most often between November and February. The species ranges from southern Mexico and the Yucatan peninsula through Central America and the West Indies to Bolivia and southern Brazil.

*Alternanthera tenella* is recognized by the small sessile heads or spikes, the stiff sharp-tipped perianth parts with prominent longitudinal ribs and thin straight hairs, lack of hairs on older parts, and low-altitude habitats. Most of our material had been identified as *A. ficoidea* (L.) R. Br. until Mears recently determined that the Linnaean basonym, *Gomphrena ficoidea*, belongs to the species now known as *Alternanthera paronychioides*.

#### AMARANTHUS Linnaeus

Herbs, rarely perennial, erect or less often prostrate, bisexual or rarely unisexual (dioecious), glabrous or minutely puberulent, often marked with red or purplish coloring, unarmed or with spines in *A. spinosus*; stipules absent. Leaves alternate and simple, petioles often long and variable in length on the same plant, laminae entire, usually thin-textured, venation pinnate with the midvein usually extending slightly beyond the lamina to form a slender mucronate tip. Inflorescences basically of small flower clusters (glomerules of condensed cymes) in the axil of a bract, glomerules solitary or more often congested on an unbranched rachis and spicate, the spikes solitary in distal leaf axils or terminal and near-terminal to form a compound panicle arrangement of spikes, the terminal spikes often twice as long as lateral spikes, each flower subtended by a bract and 2 lateral bracteoles, bracts and bracteoles usually similar in form and size. Flowers small, mostly unisexual, the male and female often borne on the same spike with the male flowers borne distally and the female near the base, sessile or subsessile, perianth (1- to 3-) 5-parted, free, equal or subequal, thin and stiff, stamens usually the same number as the perianth parts, filaments slender and free, anthers said to be 2-thecous but dehiscent by 4 slits, ovary 1-locular, the solitary ovule from a basal placenta, style very short, stigmas 2 or 3, slender. Fruit loosely enclosed within the persisting bracts and perianth parts, usually a thin-walled utricle or capsule with circumscissile dehiscence or indehiscent; seed solitary, usually cochleate-orbicular and lenticular in cross section, often dark colored and very lustrous, smooth, embryo annular.

A genus of about 50 species in both tropical and temperate areas of the world. Most of the species are pioneers on bare soil or in early successional vegetation and many have become widespread weeds. The young leaves of a number of species are used as pot herbs, and the grain amaranths (see under *A. hybridus*) have been an important source of food in some cultures (cf. J. D. Sauer in Ann. Missouri Bot. Gard. 37:561–632, 1950). Forms with larger deeply red or purple colored inflorescences have been used for ornamental planting and in floral arrangements. Members of the genus are usually recognized by the short-lived weedy growth habit, unusual panicle grouping of spikes at the apex of the plant (in most species), dense clusters of flowers and bracts, fruit loosely enclosed in the persisting perianth and bracts and usually opening by having the distal half fall away, and the small shiny lenticular seeds. The name *Bledo* is often used in Central America to refer to species of *Amaranthus*.

- 1a Plants bearing paired straight spines (5–15 mm long) from some of the leaf axils; seeds 0.7–1 mm broad; widespread plants from sea level to 1,600 m elevation *A. spinosus*
- 1b Plants lacking spines in the leaf axils.....2a
- 2a Fruiting perianth broadest above the middle and becoming partly reflexed with the distal half rotate; seeds ca. 0.9 mm broad; seasonally dry areas of the Pacific slope below 900 m elevation.....*A. scariosus*
- 2b Fruiting perianth not broadest above the middle and not becoming reflexed in fruit.....3a
- 3a Fruit indehiscent and with a rugose yellowish brown surface; perianth 3-parted, stamens 3, floral bracts 0.5–1 mm long; rachis often visible on the spikes...*A. viridis*
- 3b Fruit usually circumscissely dehiscent and with a smooth surface; perianth 5-parted, stamens usually 5, floral bracts 1.5–4 mm long; rachis usually obscure in the spicate inflorescences.....4a
- 4a Floral bracts up to twice as long as the perianth parts and usually with conspicuous spine tips; seeds more than 1 mm broad; plants of waste places near habitations or cultivated for the seed or colorful inflorescences, common on the Meseta Central, 1,000–2,000 m.....*A. hybridus*
- 4b Floral bracts equaling the perianth in length; seeds ca. 1 mm broad; weedy plants of the Caribbean lowlands.....*A. dubius*

**Amaranthus dubius** Martius ex Thellung, Mém. Soc. Sci. Nat. Cherbourg 38:203. 1912. *A. tristis* Willd., Hist. Amaranth 21. 1790, not *A. tristis* L., 1753. Figure 28.

Herbs, 0.2–1 (1.5) m tall, unisexual, branches ascending, leafy internodes 0.5–6 cm long, 1–6 mm thick, at first minutely puberulent with thin curled or scurfy hairs ca. 0.2 mm long, becoming glabrous and longitudinally ridged or sulcate. Leaves alternate, petioles 1–10 cm long, sulcate above with 2 adaxial ridges continuous with the lamina margins; laminae 3–8 (12) cm long, 2–6 (8) cm broad, ovate-rhombic to ovate-oblong or ovate elliptic, the smaller leaves elliptic, bluntly obtuse at the apex and often with a thin 1–2 mm mucronate extension of the midvein, obtuse to acute at the base and attenuate on the petiole, margin entire or slightly crenulate, laminae drying thin-chartaceous, sparsely and very minutely (0.1 mm) puberulent on the veins beneath or glabrescent, midvein impressed above, the 4–12 pairs of major secondary veins prominent beneath. Inflorescences solitary in the leaf axils or in terminal panicle arrangements, flower clusters densely aggregated along the flowering rachis forming spikes 4–9 (12) mm in diameter, terminal spikes to 15 (25) cm long, lateral spikes 0.5–6 cm long, floral bracts 1.5–2.5 mm long and usually equalling the flower in length, ovate to lanceolate and ending in a sharp tip; flowers unisexual with the male less common than the female, perianth 1.5–2 mm long, stamens 5, stigma 3. Fruit loosely enclosed within the subequal and loosely persisting bracts, bracteoles, and perianth, utricle 1.5–2.5 mm long with circumscissile dehiscence; seeds cochleate-orbicular and lenticular in cross section, 0.8–1.1 mm broad, dark brown or black and very lustrous.

Plants of open early successional sites at altitudes below 1,000 m and flowering throughout the year. The species is a common weed in the Caribbean area and ranges from Mexico to southern South America. The species has become established in Europe and Africa.

*Amaranthus dubius* is recognized by its open weedy lowland habitat, floral bracts equalling the flowers in length, and the almost circular, lenticular seeds about 1 mm broad. This species has only been collected from the Caribbean Coastal Plain in Costa Rica and may not occur above 200 m elevation in our area.

**Amaranthus hybridus** L., Sp. Pl. 990. 1753. *A. hypochondriacus* L., loc. cit. 991. 1753. Figure 28.

Herbs, 0.3–1.5 (2) m tall, erect and often much branched, bisexual, leafy internodes 0.5–3 cm long, 1–5 mm thick, sparsely puberulent with minute (ca. 0.2 mm) thin crooked hairs in early stages, becoming glabrescent and longitudinally ridged or sulcate when dry.

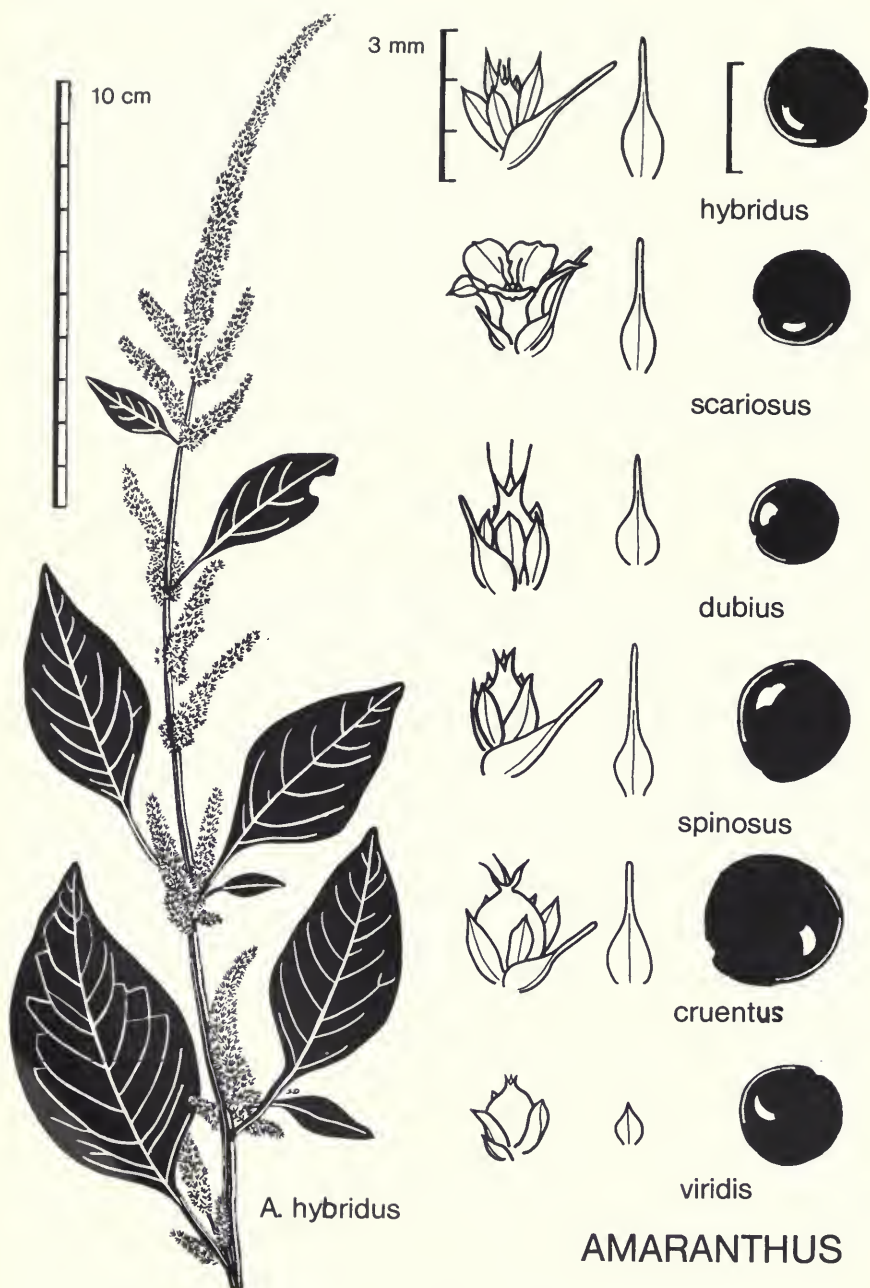


FIG. 28. Amaranthaceae: species of *Amaranthus*, after Sauer.



Leaves alternate, petioles 1–8 (12) cm long, sulcate above with 2 adaxial ridges continuous with the lamina margins, sparsely and minutely puberulent; laminae (2) 4–10 (15) cm long, 1–7 (10) cm broad, ovate to rhombic or narrowly ovate-elliptic in smaller leaves, bluntly obtuse in larger leaves or acute in smaller leaves, with a thin 2-mm extension of the midvein beyond the lamina, margins entire or slightly crenulate, lamina drying chartaceous, glabrous or very sparsely puberulent with thin crooked hairs only 0.1–0.2 mm long, midvein impressed above, the 6–10 pairs of major secondary veins pale in color and prominent beneath. Inflorescences terminal and axillary, spicate or the spikes in terminal panicle arrangements, 1–18 cm long, the individual spikes 5–15 mm thick, flower clusters closely congested and the rachis usually obscure, bracts subtending the flower clusters 2–4 mm long with almost half the length of the bract made up of a distal stiff spine, bracts mostly twice as long as the perianth parts; flowers unisexual or bisexual, perianth 5-parted, 1.3–2.3 mm long, thin, stamens 5, stigmas 3. Fruit loosely enclosed in the small persisting perianth and larger stiff bracts, a thin-walled utricle with circumscissile dehiscence near the middle; seeds 1–1.4 mm broad, cochleate-orbicular in outline and thick-lenticular in cross section, edge with a weakly defined ridge, dark reddish brown to black, lustrous.

Plants of open fields, roadsides, and early successional habitats and now naturalized throughout the world in both tropical and temperate areas. In Costa Rica, the species has only been collected between 1,000 and 1,700 m elevation near the towns and cities of the eastern part of the Meseta Central (San Pedro de Puriscal to San Jose and Cartago); probably capable of flowering at any time of the year in our area.

*Amaranthus hybridus* is recognized by the spine-tipped bracts often twice as long as the perianth parts, the minute puberulence of younger parts and leaves, long petioles, and the dark shiny seed usually more than 1 mm broad. The plants are often marked with pink, red, or purple and seem to be collected only near the more densely populated or well-traveled areas of Central America.

*Amaranthus hybridus* subsp. *cruentus* (L.) Thellung (in Asch. & Graebn., Synopsis 5:243, 1914), more often referred to as *Amaranthus cruentus* L. and also placed under *A. caudatus* L., is the commonly cultivated grain amaranth of northern Central America. These plants are grown for ornament, are occasionally used as pot herbs, and are an important grain in some areas. They differ in having more reddish coloring in the floral bracts, the larger utricle exceeding the perianth parts, the shorter floral bracts, and the lateral spikes of the terminal panicle being more divergent than those in plants of typical *A. hybridus*. The two entities, whether species or subspecies, are very closely related and, though extensively cultivated in Guatemala, we have seen no authentic material of subspecies *cruentus* from Costa Rica.

***Amaranthus scariosus* Benth., Bot. Voy. Sulph. 158, pl. 51, 1844. Figure 28.**

Herbs, 0.5–1.5 (2) m tall, erect and usually much branched, unisexual, leafy internodes 0.5–4 cm long, 1.2–6 mm thick, glabrous or the new growth with minute puberulence, stems often pink in life, terete. Leaves alternate, petioles 2–10 cm long, sulcate above with adaxial ridges continuous with the lamina margins; laminae 2–9 (12) cm long, 1–5 cm broad, ovate to rhombic or elliptic-ovate (ovate-lanceolate in smaller leaves), tapering to an obtuse apex, the midvein extended less than 1 mm beyond the lamina, obtuse to cuneate at the base and slightly decurrent on the petiole, margins entire, the laminae drying membranaceous to very thin-chartaceous, smooth and essentially glabrous above and below, midvein impressed above, the 7–12 pairs of major secondary veins pale in color and prominent beneath. Inflorescences terminal or axillary, small spikes to panicle arrangements of spikes, 0.5–25 cm long, often densely clustered on the distal part of the stem, floral bracts 2–4 mm long, subulate-lanceolate and sharp-tipped, green along the midrib, slightly exceeding the flowers; flowers unisexual, female perianth parts 5, ca. 3 mm long



and 1.5 mm broad, obovate and broadest above the middle, with a green midrib and broad translucent margins, rounded apically, stamens 5, stigmas 3. Fruit loosely enclosed within bracts and perianth, the perianth parts becoming partly reflexed and rotate in form, utricle shorter than the tubelike base of the perianth; seed ca. 0.9 mm broad, orbicular or cochleate-orbicular, thick-lenticular in cross section, smooth and very lustrous, dark brownish black.

Weedy plants of open fields and forest edges on the seasonally very dry Pacific slope of northern Costa Rica below 900 m elevation; flowering and fruiting material has been collected from late December through February. The species ranges from southwestern Mexico along the Pacific lowlands to Guanacaste Province in Costa Rica.

*Amaranthus scariosus* is recognized by its unusual female perianth parts which are broadest above the middle and become reflexed above the middle to form a tubelike lower basal part and a rotate distal part. The general lack of pubescence, long-petioled leaves, and restricted habitat in seasonally deciduous areas further distinguish this species. The species probably occurs in northernmost Puntarenas, but has not been collected outside of Guanacaste in Costa Rica. It is interesting that a plant of weedy early successional habitats has such a restricted geographical range.

***Amaranthus spinosus* L., Sp. Pl., 991. 1753. Figure 28.**

Herbs, 0.5–1.5 (2) m tall, erect and with spreading branches, bisexual, leafy internodes 0.3–5 (8) cm long, 0.7–4 mm thick (dry), smooth and glabrous or sparsely and very minutely puberulent in early stages, often reddish or purplish in life and becoming irregularly longitudinally striate when dry, paired sharp spines 8–15 mm long and ca. 1 mm thick at the base often arising from the leaf axils and oriented ca. 90° from the stem, sulcate adaxially. Leaves alternate, often variable in size on the same stem, petioles 0.5–6 (8) cm long, less than 1 mm broad (dry), slightly sulcate above with 2 adaxial ridges continuous with the laminae margins; laminae 1–10 (12) cm long, 0.6–3.5 (5) cm broad, narrowly elliptic to elliptic-lanceolate or ovate-elliptic, bluntly to sharply acute and rounded at the tip, often with a slender terminal spine 1–3 mm long, acute or obtuse at the base and decurrent on the petiole, margin entire, the laminae drying thin-chartaceous or membranaceous, smooth and glabrous, midvein impressed above with 4–7 pairs of major secondary veins drying pale in color and prominent beneath. Inflorescences terminal or from the axils of distal leaves, varying (often on the same plant) from small axillary fascicles or glomerules ca. 10 mm in diameter to densely flowered spikes 1–8 (14) cm long and 5–10 mm thick, the spikes often subtended by paired spines 3–6 mm long, bracts variable and often resembling the spines, 2–5 mm long, ovate to subulate; flowers unisexual with the male flowers at the tips of spikes and the female in the lower (proximal) glomerules, perianth 5-parted, 2–2.5 mm long in the male and ovate-oblong, 1.5–2.5 mm long and oblong-spatulate in the female, scariosus, the midvein green and margins translucent, stigmas slender, papillate-puberulent, to 1.5 mm long. Fruit loosely enclosed in the persisting perianth, utricle ca. 1.5 mm long, pale brown with circumscissile dehiscence or indehiscent; seed cochleate-orbicular, lenticular in cross section, 0.7–1 mm broad, dark brown and very shiny lustrous.

Plants of open sites and early secondary growth from sea level to 1,600 m elevation on both the seasonally dry Pacific slope and in the evergreen Caribbean formations; probably flowering throughout the year in Costa Rica, but collected primarily in June and July; collections from the deciduous lowlands of Guanacaste have been made primarily between June and January. This species is now widespread in the warmer parts of the world.

*Amaranthus spinosus* is recognized by the paired spines arising from the leaf axils, generally glabrous parts, and small seeds. An unusual collection by John Taylor (4431 NY) with the floral bracts considerably more spiny than usual and

collected on Volcan Irazu at 3,200 m elevation is included here. However, it is unlikely that populations of this species persist above 2,000 m elevation in Costa Rica.

***Amaranthus viridis* L., Sp. Pl., ed. 2, 1405. 1763. *A. gracilis* Desf., Tabl. Bot. 43. 1804. Figure 28.**

Herbs to ca. 1 m tall, erect or decumbent, bisexual, leafy internodes 0.2–3 (5) cm long, 0.8–4 mm thick, glabrous or very sparsely and minutely puberulent in early stages. Leaves alternate, petioles very slender (dry), 0.3–10 cm long, often very variable in length on the same plant, slightly sulcate above with adaxial margins continuous with laminae margins; laminae 0.5–5 (7) cm long, 0.3–3 (4) cm broad, ovate to bluntly triangular or rhombic, elliptic or elliptic-ovate, rounded at the bluntly obtuse apex and emarginate at the tip with the midvein extended less than 1 mm beyond the lamina, abruptly narrowed or rounded at the obtuse to subtruncate base, decurrent on the petiole, margin entire or slightly crenulate when dry, the laminae drying very thin-chartaceous, smooth and glabrous, with 4–8 pairs of major secondary veins prominent below. Inflorescences usually solitary, terminal or in the axils of distal leaves, spikelike with clusters of flowers borne on an unbranched axis, spikes 1–8 (12) cm long, 3–7 mm thick, flower clusters often separate and the rachis visible, floral bracts and bracteoles subequal, 0.5–1 mm long, thin and scarious; flowers unisexual, longer than the bracts, perianth 3-parted, 1–1.5 mm long, stamens 3, stigmas 3. Fruit a rugose utricle clearly exceeding the persisting perianth and bracts, ca. 2 mm long, indehiscent, pale yellowish brown; seed 0.9–1 mm broad, cochleate-orbicular in outline, thick-lenticular, very dark brown or black, moderately lustrous, with a weakly defined ridge around the margin.

Small weedy plants of open sandy and gravelly soils and often seen as pioneers on bare soil from near sea level to 1,500 m elevation; probably capable of flowering throughout the year in our area. This species is a pantropical weed.

*Amaranthus viridis* is recognized by its very small stature, glabrous parts, small bracts and bracteoles, 3-parted perianth, and indehiscent fruit with rugose surface. These plants are often found as pioneers on open soil, but they appear to be quite rare in our area, with only a few collections from Guanacaste and the eastern side of the Meseta Central.

### CELOSIA Linnaeus

Annual or perennial herbs or subshrubs, erect (in ours) to sarmentose or climbing, bisexual, glabrous to sparsely puberulent. Leaves alternate, often decurrent on the stem, petioles often with lateral margins gradually expanding into the lamina margins; laminae entire and pinnately veined. Inflorescences usually dense spikes (heads), axillary or terminal, solitary, or variously disposed in panicate arrangements, the spikes usually sessile, the panicles sessile or pedunculate, the axes bearing the spikes usually unbranched in our species, each flower subtended by a bract and 2 lateral bracteoles. Flowers bisexual, sessile or subsessile, perianth of 5 free and equal or subequal parts, scarious, longitudinally ribbed and slightly convex, persisting but not enlarging in fruit, stamens 5, the filaments united at the base to form a cup shorter than the ovary, anthers 4-celled, and introrse, ovary globose to ellipsoid, 1-locular, with several to many ovules on a basal placenta, style short to long, with 2 or 3 stigmas. Fruit a capsule, usually with circumscissile dehiscence, loosely included within the persisting bracts and perianth parts; seeds (1) 2 to many, usually cochleate-lenticular to reniform, smooth and usually lustrous, brown to black, the embryo annular.

A genus of about 40 species, mostly in Asia and Africa with only the following two species to be expected in southern Central America. Young leaves and shoots of *C. argentea* are sometimes used as vegetables, though the plants are mostly cultivated for ornament. The native species of the genus are apparently quite local or rare in Central America.

- 1a Plants grown for ornament, rarely escaping; inflorescences colorful white to rose red or magenta spikes, 5–25 cm long and 1.5–3 cm thick, flowers ca. 8 mm long  
*C. argentea*
- 1b Plants known in Costa Rica only from the deciduous forest formations of northeastern Guanacaste Province; inflorescences of small greenish spikes, 0.5–3 cm long, often borne in panicle arrangements, flowers ca. 5 mm long . . . . . *C. virgata*

***Celosia argentea* L., Sp. Pl. 205. 1753. *C. cristata* L., loc. cit. Figure 29.**

Annual herbs, erect, 0.2–1 (rarely 2) m tall, branched or unbranched, leafy internodes 0.5–9 cm long, 1–7 (12) mm thick, glabrous, becoming longitudinally ridged or grooved. Leaves alternate in a spiral, petioles 4–30 mm long, with lateral margins that expand gradually to the lamina margins, decurrent on the stem; laminae 3–15 cm long, 0.5–6 cm broad, ovate to ovate-elliptic or narrowly lanceolate, acute to acuminate at the apex, tapering gradually or abruptly to the base and decurrent on the petiole, margins entire, the laminae drying stiffly chartaceous, glabrous, the 5–8 pairs of major secondary veins strongly ascending. Inflorescence usually terminal and solitary or a few clustered together, usually a densely flowered thick (1–2 cm) spike, 1.5–15 (25) cm long, occasionally with abnormal (fasciated) growth patterns and broadly expanded or divided at the apex, peduncles glabrous, 0.3–12 cm long, floral bracts ca. 6 mm long, lanceolate, lustrous whitish to pinkish, decurrent on the rachis, carinate and mucronate; flowers 8–10 mm long, subsessile to short (2 mm) pedicellate, perianth thin and dry (scarious), lustrous, silvery white to deep rose red, 6–9 mm long, persisting in fruit, style 3–6 mm long, usually exceeding the perianth. Fruit a circumscissile capsule, 3–4 mm long, hidden within the persisting perianth and bracts, with (1) 3–9 seeds per fruit; seeds 1.5–2 mm broad, cochleate-lenticular, very lustrous, black or dark reddish brown.

Plants grown in gardens for their colorful inflorescences and only rarely escaping (especially along streams); flowering throughout the year and rarely encountered above 1,400 m elevation in Central America. The species is of uncertain origin and is now widely cultivated throughout the tropics.

*Celosia argentea* is recognized by its alternate leaves with laminae decurrent on the petioles, glabrous parts, and thick colorful spikes with stiff dry persisting bracts and perianth parts. The long-lasting lustrous white to deep rose red inflorescences make these plants very useful for floral arrangements. In some plants, the inflorescences develop a broad flattened form that may be digitate or ruffled. This form is often called variety *cristata* (L.) Voss, the "Garden cockscomb." Among the names associated with these plants in Central America are *Abanico*, *Amaranto*, *Amor seco*, *Boria*, *Cresta de gallo*, *Flor de mano*, *Mano de león*, *Moño*, *Moño de reina*, *Rabo de gato*, and *Terciopelo*.

***Celosia virgata* Jacq., Coll. Bot. 2:279. 1788, or a closely related species. Figure 29.**

Erect herbs, 0.5–1.5 m tall, leafy internodes 5–80 mm long 1–4 mm thick, glabrous or minutely (0.5–2 mm) puberulent with thin crooked hairs, quickly becoming glabrous. Leaves alternate in a spiral, decurrent on the stems, petioles 1–8 cm long, with lateral margins gradually expanding to the lamina base; laminae 3–15 cm long, 1–6 cm broad, ovate to ovate-elliptic or the smaller leaves often lanceolate, acute to short-acuminate at the apex, often with a sharp tip 1–3 mm long, acute to obtuse at the base and decurrent on the petiole, margin entire, drying thin-chartaceous, laminae essentially glabrous, with 5–7 pairs of major secondary veins. Inflorescences basically of short (8–20 mm) spikes, solitary and axillary to terminal and variously clustered, the panicle clusters usually with a single primary axis 5–20 cm long and with separate or congested spikes alternating along the axis (our material differs from all other collections of the species in having slender peduncles or with a 2–5 cm long spike-free basal portion on the inflorescence axis, similar peduncles in other collections rarely exceed 2 cm), bracts and lateral bractlets subequal, 2–3 mm long, cuspidate with a single midvein and thin hyaline margins, nar-



FIG. 29. Amaranthaceae: Costa Rican representatives of the genera *Celosia*, *Chamissoa*, and *Pleuropetalum*.



rowly triangular to lanceolate; flowers subsessile, ca. 5 mm long, perianth parts with 3–7 abaxially prominent longitudinal ribs in the basal half, oblong-lanceolate. Fruit with (1) 3–8 seeds, utricle shorter than the perianth parts; seeds 0.7–1 mm broad, cochleate-lenticular, black, lustrous.

Uncommon herbs found in both moist evergreen and in seasonally very dry deciduous formations, from near sea level to 700 m elevation (rarely to 1,200 m); flowering and fruiting collections have been made from September to March in Central America. The species ranges from central Mexico through Guatemala, El Salvador, Honduras, and has recently been collected near Santa Rosa in north-western Guanacaste Province, Costa Rica.

*Celosia virgata* (in a wide sense) is characterized by its short stature, alternate leaves with laminae decurrent on the petiole, general lack of pubescence, inflorescences composed of short spikes often aggregated on unbranched axes, single-veined translucent bracts, stiff multiple-ribbed perianth, and small distinctive shiny seeds. A single recent Costa Rican collection by Ronald Liesner (4303) is tentatively placed here. It differs from most specimens of the species in a number of ways: The leaf axils do not have the little axillary leaves usually found in the species, the inflorescences of the Costa Rican collection have clearly defined peduncles, and there are apparently fewer but slightly larger seeds in each fruit. Nevertheless, stature, leaves, bracts, and flowers are virtually identical to those of typical Mexican and Guatemalan collections. It may be that the plants from near Santa Rosa are worthy of subspecific recognition.

#### CHAMISSOA Humboldt, Bonpland & Kunth

REFERENCE: S. H. Sohmer, A revision of *Chamissoa*. Bull. Torrey Bot. Club. 104:111–126, 1977.

Shrubs, subshrubs, or lianas, usually climbing or clambering over adjacent vegetation, stems glabrous or puberulent, terete; stipules absent. Leaves alternate and simple, petiole, entire or slightly undulate, pinnately veined, glabrous or sparsely puberulent. Inflorescences terminal or axillary, solitary, leaves of the upper (distal) nodes often undeveloped and the inflorescence a compound panicle, the flowers borne in small cymes of 2–20 flowers, the cymes usually on unbranched axes and in arrangements of spicate branches, the flowers subsessile or very short-pedicellate and subtended by a bract and 2 lateral bracteoles, bract and bracteoles subequal, persistent and becoming stiff and dry; flower small and radially symmetrical, bisexual or functionally unisexual, perianth of 5 ovate-lanceolate imbricate parts, stiff and persisting but not enlarging in fruit, stamens 5, united near the base to form a short tube, pseudostaminodial appendages absent, pistil with 1 locule and 1 ovule from a basal placenta, style 1 with 2 slender stigmas. Fruit a thin-walled capsule opening by circumscissile dehiscence near the top (a pixedium); seeds lenticular, black or marked, embryo small with much endosperm.

A genus of two species ranging from Mexico through the West Indies and Central America to nearly all of South America excepting Chile and southern Argentina. The alternate leaves, unusual fruit, and dense inflorescences made up of racemose or spicate arrangements of cymes help distinguish the genus.

- 1a Plants clambering or climbing, often becoming lianas over 2 m high; seeds enclosed by 2-valved arils; flowers bisexual or female, ovary over 2 mm long, tubular or oblong in form; common lowland plants. . . . . *C. altissima*
- 1b Plants erect or clambering over others, up to 2 m tall but never becoming lianas; seeds with minute and inconspicuous arils; flowers always bisexual, ovary usually less than 2 mm long, ovate to globose in form; plants only rarely collected in Central America. . . . . *C. acuminata*

***Chamissoa acuminata*** Martius, Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 13:286. 1826.

Herbs or subshrubs, erect or clambering, 1–2 m tall, leafy internodes ca. 3–6 cm long, slender and glabrescent in ours. Leaves alternate, petioles 1–3 (7) cm long, slender; laminae 3–11 (14.5) cm long, 1–4 cm broad, narrowly ovate to lanceolate, tapering gradually to the acute or acuminate apex, rounded to obtuse at the base, margins entire, glabrous or puberulent, with 3–7 pairs of major secondary veins. Inflorescences terminal or axillary, 1–6 (30) cm long, usually simple and spikelike, sometimes compound and paniculate, glomerules with 3–7 flowers, bracts and bracteoles 1.5–2.5 mm long, perianth and bracts greenish white or yellowish, perianth 5-parted, 2.4–4 mm long, ca. 1 mm broad; stamens 5; ovary ovate to globose, 1.5–2.3 mm long, style 0.5–1.5 mm long, dilated at the base, stigmas shorter than the style. Fruit a capsule, usually opening by a circular lid; seed 1.5–2.5 mm long, black and lustrous.

Though ranging from southern Mexico to Bolivia and Paraguay, this species has not been collected in Costa Rica. The type collection of *C. acuminata* var. *swansonii* Sohmer comes from Bocas del Toro, Panama (Wedel 1695), and our plants should be identical.

*Chamissoa acuminata* is very similar to *C. altissima*, but does not become a liana and differs in floral structure. In addition, the flowers seem to be less robust, and the stems usually are more slender.

***Chamissoa altissima*** (Jacq.) H.B.K., Nov. Gen. & Sp. 2:197, pl. 125. 1817. *Celosia paniculata* L., Sp. Pl. ed. 2, 298, not L., 1753. *Achyranthes altissima* Jacquin, Enum. Pl. Carib. 17. 1762. *Chamissoa macrocarpa* H.B.K., Nov. Gen. & Sp. 2:197. 1817. Figure 29.

Clambering shrubs to 2 m tall or woody vines to over 10 m long, leafy internodes 2–10 cm long, 1–4 mm thick, very sparsely puberulent with minute (0.1–0.5 mm) hairs, becoming longitudinally striate when dry. Leaves alternate and usually in a spiral, petioles 0.5–3 (7) cm long, 0.5–1.5 mm broad, very sparsely and minutely puberulent, sulcate above with adaxial ridges continuous with the laminae margins; laminae 3–15 (19) cm long, 1.5–7 (9) cm broad, narrowly ovate to broadly ovate or lanceolate, tapering gradually to the acute or acuminate apex, acute to obtuse or truncate at the base, often rounded and truncate in larger laminae, margins entire or slightly undulate, somewhat decurrent on the petiole, the laminae drying thin to stiff chartaceous, smooth on both surfaces, very sparsely puberulent with minute whitish hairs with 3–6 pairs of major secondary veins. Inflorescences basically small cymules densely clustered on a spikelike rachis 1–15 cm long, the spikelike axes solitary and axillary or in complex terminal paniculate arrangements formed by the failure of distal leaves to develop, the cymules short (1–3 mm) pedunculate and bearing 2–8 (20) flowers, flowers very short pedicellate and subtended by a bract and 2 lateral bracteoles; flowers yellowish to white or greenish white to rose, perianth parts 2–3 (5) mm long, stamens with filaments 2–3 mm long, anthers very small (0.2 mm) in functionally female flowers, to 1 mm long in functionally male flowers, pistil 2–3 mm long in functionally female flowers, style 0.4–1 mm long, the 2 linear stigmas minutely papillose. Fruit 3–4 mm long, 1.5–2 mm broad, somewhat ellipsoid with truncated apex and base, opening with a circular lid near the top; seeds lenticular, orbicular in outline, ca. 2 mm broad, black and lustrous.

Climbing or clambering plants of both the evergreen wet and seasonally very dry deciduous formations from sea level to 1,500 m elevation, but most common below 300 m; while occasional flowering plants have been found from May to November, the majority of flowering and fruiting collections have been made from December to April. The species ranges from Mexico through Central America and the West Indies to northern Argentina.

*Chamissoa altissima* is recognized by the vining or clambering sparsely puberulent stems with alternate thin-petioled leaves, spicate or paniculate arrange-

ments of densely or loosely aggregated flower clusters, flowers with stiff persisting pale-colored perianth and bracts, and the thin-walled fruit that opens by a circular lid near the top bearing a short style and 2 stigmas. Plants with flowers pinkish red to dark purple or with reddish ovaries often having three stigmas have been designated as variety *rubella* by Sohmer.

### CYATHULA Loureiro

Herbs or subshrubs, annual or perennials, erect, prostrate, or decumbent, usually developing a woody base and often with long internodes, bisexual; stipules absent. Leaves opposite and simple, petiolate, laminae entire and pinnately veined. Inflorescences terminal or axillary, solitary or 3 at terminal nodes, spicate with a single unbranched axis bearing very short-pedunculate flower fascicles (glomerules), the fascicles with 1 to several fertile bisexual flowers and perianth parts and bracts of highly modified sterile flowers, the fascicles spicate or capitate and usually subtended by a bract and several bracteoles of similar size, bracts and bracteoles usually aristate, parts of the sterile flowers developing elongate spines or bristles ending in sharp hooks as the fruit develop; functional flowers bisexual, small and radially symmetrical, perianth of 5 free subequal, imbricate parts, stiff and persisting but not enlarging in fruit, with 1–5 longitudinal ribs, stamens 5, united at the base to form a tube with small pseudostaminodial appendages, anthers 4-thecous, dehiscent introrse, ovary ovoid to obovoid, 1-locular, the solitary ovule pendulous from a long funicle arising from a basal placenta, style 1 with capitate stigma. Fruit an indehiscent utricle, tightly enclosed by the stiff persisting perianth; seeds reniform-oblong to cochleate-orbicular, testa lustrous brown.

A genus of about 20 species probably native to the tropics of Asia and Africa, with two species introduced into the neotropics. Our members of the genus are recognized by their small weedy habit, opposite sparsely sericeous leaves and long spikelike inflorescences with unusual flower fascicles that become reflexed on the spike and develop elongate spines with hooked tips in later stages. These plants resemble and are closely related to *Achyranthes*.

- 1a Fruiting fascicles developing 5–15 hooked spines to 4 mm long, perianth parts ca. 4 mm long; seeds to 2 mm long; terminal spikes becoming 1–2 (4) × as long as the subtending leaves; larger laminae usually over 6 cm long, narrowly elliptic and long acuminate ..... *C. achyranthoides*
- 1b Fruiting fascicles developing over 20 hooked spines to 2 mm long; perianth parts 2–3 mm long; seeds 1–1.5 mm long; terminal spikes becoming 2–10 × as long as the subtending leaves, larger laminae usually less than 7 cm long, usually rhombic and obtuse to acute at the apex ..... *C. prostrata*

***Cyathula achyranthoides*** (H.B.K.) Moq., in DC., Prodr. 13, pt. 2:327. 1849.  
*Desmochaeta achyranthoides* H.B.K., Nov. Gen. & Sp. 2:210. 1817. Figure 25.

Herbs or subshrubs to 1 (2?) m tall, erect or decumbent and rooting at the lower nodes, leafy internodes 2–18 cm long, 1–4 mm thick, sparsely puberulent with thin ascending sericeous hairs, more densely puberulent at the nodes. Leaves opposite and decussate, petioles 2–6 (10) mm long, appressed puberulent, with lateral margins continuous with the lamina margins; laminae 3–15 (20) cm long, 1.5–5 (7) cm broad, the larger laminae elliptic to narrowly elliptic and tapering gradually to both apex and base, the smaller laminae more abruptly tapering and often rhombic-ovate, acuminate to acute at the apex (in larger laminae) acute or obtuse to attenuate at the base, margin entire or slightly undulate and decurrent on the petiole, laminae drying thin- to stiff-chartaceous, smooth to the touch above and below, sericeous with thin whitish appressed-ascending hairs 0.5–2 mm long on both surfaces but usually more dense beneath, with 4–7 pairs of major secondary veins. Inflorescences terminal or axillary, spicate, 5–20 cm long, 5–10 mm broad, peduncle 0.5–8 cm long with thin whitish hairs ca. 0.5 mm long, bracts subtending the flower fascicles (glomerules) 1.5–3 mm long, thin-translucent and broadly lanceolate, mucronate or aris-



tate, each fascicle borne on a very short (0.5 mm) peduncle and becoming reflexed, the flower fascicles tending to remain closely adjacent even in fruit, the fascicle or glomerule usually with 1 fertile flower and 1 sterile flower, the hooked (uncinate) spines 1–4 mm long and often exceeding the perianth; flower with the perianth parts ca. 4 mm long and 1.5 mm broad, strongly ribbed and sparsely puberulent with thin whitish hairs. Fruit very difficult to separate from the enclosing perianth, utricle ovoid and operculate, 1.5–2.5 mm long; seeds somewhat oblongoid, reniform to cochleate-orbicular, 1.5–2 mm long, ca. 1 mm thick, lustrous brown.

Plants of open or partly shaded sites in both moist evergreen and seasonally very dry formations, from sea level to 1,000 m elevation but rarely collected above 700 m; flowering and fruiting throughout the year in Costa Rica, but collected most often from November to May. In seasonally very dry Guanacaste, the collections are primarily from December and January. The species ranges from Mexico and the West Indies to Brazil and throughout much of central Africa.

*Cyathula achyranthoides* is recognized by the spikelike inflorescences with densely crowded flower fascicles (glomerules) that become reflexed on the spikes and develop five to 15 stiff hooked spines. The plants are usually found in recently disturbed areas or early secondary growth in both open and shaded sites. The plants are most common in the Caribbean lowlands (0 to 200 m).

***Cyathula prostrata* (L.) Blume, Bijdr. Ned. Ind. 549. 1826. *Achyranthes prostrata* L., Sp. Pl. ed. 2, 296. 1762. Figure 25.**

Herbs or subshrubs, 0.2–0.8 (1) m tall, erect or procumbent, leafy internodes 2–15 cm long, 0.6–3 mm thick, sparsely puberulent with thin spreading or ascending whitish hairs 0.3–1.5 mm long, stems 4-angled or with 4 longitudinal ridges. Leaves opposite and decussate, petioles 2–12 mm long, with narrow lateral margins continuous with the lamina margins, sparsely puberulent; laminae 1–6 (8) cm long, 0.8–4 cm broad, broadly elliptic to rhombic, obtuse to acute at the apex and rounded or obtuse at the base, margin entire and decurrent on the petiole, the laminae drying thin to stiff chartaceous, smooth on both surfaces, sparsely strigillose above and below with thin usually straight ascending hairs 0.3–1 mm long, with 3–5 pairs of major secondary veins. Inflorescences terminal or axillary, solitary or 3 at a terminal node, spicate, 5–20 (30) cm long, 4–8 mm broad, elongating in fruit, peduncles 2–5 cm long, the flower fascicles (glomerules) at first tightly congested and spreading but becoming separate and reflexed on the narrow (1 mm) sparsely puberulent rachis, the flower clusters borne on short (0.2–1 mm) peduncles and subtended by short (1 mm) lanceolate hyaline bracts, usually with 3 bisexual flowers and 2–4 mm long, hooked (uncinate) awns developing as the fruit matures, 1–2 mm long and not usually exceeding the fascicle in length, often more than 20 per fascicle; flowers with perianth parts 2–3 mm long, composed of 5 scarious subequal parts. Fruit tightly enclosed within the stiff persisting perianth parts, utricle ovoid, 1–2 mm long, inconspicuously operculate; seeds slightly flattened and reniform to cochleate-orbicular, ca. 1 mm long.

Weedy plants of open or shaded sites in disturbed areas, stream beds, and early successional vegetation in wet and moist evergreen formations between sea level and 1,000 m elevation; probably flowering throughout the year, but with no collections having been made from July to October. The species (probably introduced) has a discontinuous range from Mexico and the West Indies to Brazil; the species ranges widely across central Africa, tropical Asia, and Oceania.

*Cyathula prostrata* is recognized by the long spicate inflorescences, with fascicles of flowers that become separate and reflexed on the rachis, and the later development of many short hooked spines in each flower fascicle. The small stature of the plants, their angled stems, small opposite leaves, and the short stiff perianth that protects the fruit are also characteristic. The plants are often found along stream edges in evergreen formations in our area.



## GOMPHRENA Linnaeus

REFERENCE: J. A. Mears, The Linnaean species of *Gomphrena* L. Taxon 29:85–95, 1980.

Annual or perennial herbs, prostrate or erect, stems sometimes slightly thickened at the nodes, usually puberulent with thin unbranched multicellular hairs. Leaves opposite, sessile or petiolate, simple and entire, often with a small spine at the lamina apex, usually puberulent. Inflorescences terminal or axillary, solitary or less often clustered, sessile, heads or short thick spikes, the bracts, bracteoles, and flowers densely crowded together, each flower subtended by a single abaxial bract and 2 lateral bracteoles, the bracteoles usually much larger than the bracts, bracteoles concave and often with a wing or crest developed from the dorsal (abaxial) side of the midrib, flowers bisexual, sessile, perianth of 5 equal or subequal perianth parts, wooly (lanate) hairs usually borne on the base of the perianth and enlarging in fruit, stamens 5, filaments completely united to form a tube with the anthers sessile near the apex of the tube, 2-lobed pseudostaminodia usually present at the apex of the tube between the anthers, ovary superior, locule 1, ovule solitary, style 1 with 2 slender stigmas. Fruit an indehiscent utricle, usually tightly included within the persisting bracteoles and perianth; seeds cochleate-orbicular, smooth, embryo annular.

A pantropical genus of nearly 100 described species. Our species of *Gomphrena* are easily recognized by their dense heads and spikes subtended by two small leaves and by the unusual dorsal crests on the upper half of each of the paired lateral bracteoles. These dorsal (abaxial) crests are serrate or crenate along their margins. A similar species, *G. filaginoides* Mart. & Gal., with small (1 to 3 cm) leaves and white heads almost 2 cm broad, has recently been collected in Honduras and Nicaragua. *Gomphrena elegans* Mart. and *G. tuerckheimii* (Vatke) Uline & Bray have been reported from Guatemala and Honduras, but not Nicaragua. These last two species are quite similar, with terminal heads that are not subtended by small leaves and bracteoles that do not obscure the flowers or bear conspicuous dorsal crests. These last two species look very much like some of our species of *Alternanthera* (q.v.).

- 1a Flower heads not subtended by a pair of small opposite leaves, the paired lateral bracteoles lacking conspicuous dorsal crests, tips of the flowers usually visible within the bracteoles. Weedy plants of northern Central America but not yet collected from Costa Rica. See the discussion under the genus and compare with species of *Alternanthera*.
- 1b Flower heads of spikes subtended by a small pair of leaves, the paired lateral bracteoles with conspicuous serrate to crenate dorsal crests, flowers hidden within the bracteoles both in flower and fruit. . . . . 2a
- 2a Plants commonly grown in gardens and used in floral arrangements; heads of spikes ca. 2 cm thick, often bright pink or magenta, flowers and bracteoles long-persisting  
*G. globosa*
- 2b Plants native weeds of open sunny sites below 1,300 m elevation; floral heads or spikes ca. 1 cm thick, usually white, older flowers and bracteoles deciduous and only the smaller (3 mm ) floral bracts persisting on the lower portion of older inflorescences  
*G. serrata*

***Gomphrena globosa* L., Sp. Pl. 1:224. 1753.**

Erect or ascending annual herbs to 1 m tall. Leaves opposite, laminae 2–10 cm long, 0.5–4 cm broad, narrowly elliptic to elliptic-oblong, acute at the apex with a small spine tip, with thin ascending appressed hairs on both upper and lower surfaces. Inflorescences solitary and terminal or rarely paired and axillary, globose heads or thick (2 cm) short (2–4 cm) spikes, the heads or spikes subtended by small (0.5–2 cm) ovate leaves, the primary floral bracts small (3 mm) and hidden by the much larger (7–12 mm) lateral bracteoles, the paired lateral bracteoles with broad dorsal crests arising from the upper half of the midrib (abaxially), the crests irregularly crenate-serrate. Flowers hidden within the bracteoles,

perianth parts 5–8 mm long, stamens forming a tube 4–8 mm long. Fruit an indehiscent utricle tightly enclosed within the persisting perianth and bracteoles; the seed cochleate-orbicular, flattened on the sides, 1.5–2 mm broad, reddish brown.

Plants commonly grown as ornamentals in Central America and flowering throughout the year. The species is not known to have become naturalized in Costa Rica. The flower heads vary from pink and white to magenta or pink-purple in color, and because they persist long after flowering, retaining both their color and form, they are often used in floral arrangements. Common names are *Amor seco*, *Botón*, *Inmortal*, *San Diego*, and *Siempreviva* in Central America. "Batchelor's button" and "Globe amaranth" are common English names. This species is widely cultivated in the tropics and subtropics.

***Gomphrena serrata* L., Sp. Pl. 224. 1753. *G. decumbens* Jacq., Pl. Hort. Schoenbr. 4:41, t. 482. 1804. *G. dispersa* Standl., Contr. U.S. Natl. Herb. 18:91. 1916. Figure 26.**

Small herbs 10–50 (80) cm tall, prostrate or erect, annual or perennial, leafy internodes 1–15 cm long, 0.6–2 (3) mm thick, sparsely to densely sericeous with thin ascending multicellular whitish hairs 1–3 mm long. Leaves opposite, often sessile, somewhat articulate at the base, petioles 2–6 mm long, ca. 1 mm broad, little differentiated from the lamina, with 2 lateral margins continuous with the lamina margins; laminae 1.5–5 (7) cm long, 0.5–2 cm broad, narrowly elliptic to elliptic or ovate-elliptic, obtuse to acute at the apex, often with a short (0.5–1 mm) sharp stiff tip, the lamina decurrent on the petiole, entire, drying chartaceous, sparsely to densely sericeous above and below with thin ascending hairs 1–3 (4) mm long, venation pinnate with 2 or 3 pairs of major secondary veins. Inflorescences terminal and solitary (rarely 2), usually subtended by a pair of small (5–15 mm) leaves, internode below the inflorescence and its subtending leaves (peduncle if the leaves are considered bracts) 1–10 cm long, heads or becoming spikes as much as 3 cm long with the earlier basal flowers and their lateral bracteoles deciduous but the smaller (2–3 mm) bracts persisting, the smaller bracts thin whitish translucent with thickened midrib forming a sharp mucronate tip, bracteoles 4–6 mm long, stiff whitish (rarely pinkish) with an apically broadened serrate crest on the back (abaxially) of the midrib; flowers equaling or somewhat smaller than the bracteoles and included within them, perianth parts ca. 4 mm long and very narrow above the base, with a dense mass of villous-lanate hairs on the lower third, ovary tightly enclosed within the perianth. Fruit enclosed within the persisting bractlets and tightly enclosed within the thin stiff perianth parts, the lanate hairs becoming 3 mm long; seed lenticular with flattened sides, cochleate-orbicular in outline, ca. 1.3 mm long, lustrous brown, with an apical notch.

Common weedy plants of open secondary sites in both wet evergreen areas and in seasonally dry deciduous formations from sea level to 1,200 m elevation in Costa Rica; flowering throughout the year, but collected infrequently in the dry season (February to May). The species ranges from the southern United States through Central America and the West Indies to Bolivia and Argentina.

*Gomphrena serrata* is recognized by its short (sometimes prostrate) habit, slender thin ascending hairs on almost all parts, small opposite leaves with sharp tips, dense whitish heads and spikes with characteristic bracts and larger lateral bracteoles with dorsal serrate crests, and the flowers with a dense woolly covering of cotton-like hairs. These are common weedy plants of open sunny sites not collected from above 1,200 m elevation in our area. The distinctions used to separate *G. serrata* and *G. dispersa* do not appear to be consistent or important in collections seen from southern Central America. These plants resemble some of our species of *Alternanthera*, but the large paired lateral bracteoles with dorsal crests immediately distinguish this species.

IRÉSINE P. Browne

Herbs, shrubs, lianas, or rarely trees, erect or often clambering over other vegetation, unisexual or bisexual, internodes terete or strongly ridged, usually puberulent in early stages, an interpetiolar line or ridge often present and the nodes usually thickened in age. Leaves opposite or subopposite but often becoming alternate in the inflorescence, petioles with adaxial ridges continuous with the lamina margins; laminae simple and entire or rarely denticulate, usually decurrent on the petiole, venation pinnate, surfaces smooth and rarely completely glabrous. Inflorescences terminal on the main stem or terminal on distal axillary shoots, paniculate, usually large and with several orders of open distant branching, basal branches often subtended by small narrow leaves, whitish or pale yellowish, the flowers usually borne in small bracteate puberulent spikes, each flower subtended by a basal bract and 2 lateral bracteoles, bracts and bracteoles equal or dissimilar, puberulent or ciliolate. Flowers bisexual or unisexual, monomorphic or dimorphic, sessile or subsessile, perianth of 5 equal imbricate parts, narrowly oblong to lanceolate, often puberulent distally, stamens usually 5 (4, 3) united near the base to form a shallow cup, ovary narrowed at the base, style short with 2 or 3 slender or deltoid stigmas. Fruit an indehiscent utricle loosely or tightly enclosed by the persisting perianth and bracteoles, conspicuous tufts of whitish hairs often developed from the base of the perianth abaxially; seed cochleate-orbicular, thin- or thick-lenticular in cross section, smooth, pale to very dark in color, often shiny-lustrous.

*Iresine* is a genus of perhaps 40 species closely allied to *Pfaffia* and greatly in need of revision. The often unisexual flowers and the variation in size, arrangement, and pubescence of inflorescences, floral bracts, and floral parts all contribute to making specific delimitation difficult. The tufts of hairs in female and fruiting flowers develop from between the base of the perianth parts and the floral bracts, not from the interior of the perianth as in *Pfaffia*. Two species, *I. diffusa* (formerly *I. celosia*) and *I. calea*, are very common in secondary growth throughout Central America.

KEY TO THE SPECIES OF *Iresine*

- 1a Flowers unisexual and only 0.5–1.5 mm long, whitish, subtended by bracts 0.3–1 mm long; inflorescences to over 50 cm long but usually less than half as broad, branches of the inflorescences mostly alternate, very common herbs or weak shrubs of evergreen and partly deciduous formations from near sea level to 2,600 m elevation  
*I. diffusa*
- 1b Flowers 1.2–2 mm long, unisexual or bisexual, subtended by bracts 0.3–2 mm long; breadth of the inflorescence usually more than half the length, distal branches of the inflorescence opposite or alternate; herbs, shrubs, clambering shrubs or lianas . . . 2a
- 2a Spikes and flower clusters densely puberulent, branches of the inflorescence densely sericeous, usually opposite throughout . . . 3a
- 2b Spikes and flower clusters sparsely puberulent, branches of the inflorescence glabrous to sparsely and minutely puberulent, usually alternate on the primary divisions of the inflorescence; stigmas slender . . . 4a
- 3a Common plants of the Pacific slope and Central Highlands from 0–1,800 m elevation; inflorescences usually with opposite branching; flowers unisexual and dimorphic, whitish, stigmas linear; laminae with 4–8 pairs of major secondary veins . . . *I. calea*
- 3b Rare plants of wet forests formations at middle elevations; inflorescence-branching strictly opposite; flowers apparently bisexual, drying pale yellowish brown, stigmas rounded; laminae with 7–12 pairs of major secondary veins  
*I. costaricensis*
- 4a Leaves linear-lanceolate to ovate-lanceolate, with 3–8 pairs of major secondary veins; flowers bisexual; slender stemmed herbs and subshrubs (rarely clambering), on the seasonally dry Pacific slope below 800 m elevation . . . *I. angustifolia*
- 4b Leaves ovate to ovate-lanceolate, with 6–13 pairs of major secondary veins; flowers functionally unisexual; clambering shrubs and vines of wet forest formations between ca. 1,000 and 2,000 m elevation . . . *I. arrecta*



FIG. 30. Amaranthaceae: some species of *Iresine*.



***Iresine angustifolia*** Euphrasen, Beskr. St. Barthel. 165. 1795. *I. elatior* Rich., in Willd., Sp. Pl. ed. 4, 766. 1805. Figure 30.

Herbs or shrubs with slender stems, usually erect, 0.5–1.5 (2) m tall, bisexual, leafy internodes 1–14 cm long, 1–4 mm thick, glabrous or very sparsely and minutely puberulent, usually with 4 or 6 longitudinal ridges, the older nodes often thickened and sometimes with tufts of hairs in the leaf axils. Leaves opposite or subopposite, petioles 5–25 mm long, 0.5–1 mm thick, with adaxial ridges continuous with the lamina margins, glabrous; laminae 2–12 (17) cm long, 0.5–3.5 (6) cm broad, linear-lanceolate to lanceolate or narrowly ovate-lanceolate, tapering gradually to the acute or acuminate apex, tapering gradually to the acute or obtuse base, margins entire and decurrent on the petiole, the laminae drying thin chartaceous, smooth, glabrous or sparsely puberulent with short very thin and inconspicuous hairs, with 3–8 pairs of major secondary veins. Inflorescences terminal on the main stem or axillary from distal branches, paniculate, 10–50 cm long, branches of the inflorescence usually subtended by progressively smaller leaves, the flowers borne on small pedunculate spikes or in small subsessile fascicles, flower-bearing rachis puberulent, basal bracts ca. 0.5 mm long, lateral bracteoles ca. 1.5 mm long and broadly ovate, translucent and drying pale yellowish brown, slightly mucronate; flowers bisexual, sessile, perianth parts 1.0–1.8 mm long, acute at the apex. Fruit loosely enclosed in the persisting perianth, long (3–4 mm) white hairs often developed from between the base of the perianth parts and bracteoles; seed cochleate-orbicular, 0.6–0.8 mm in diameter, lenticular in cross section, black or very dark brown, shiny-lustrous.

Uncommon plants of secondary growth, forest edges, and open sites, from near sea level to 500 (800) m elevation on the seasonally dry Pacific side of Costa Rica; possibly flowering throughout the year, but with most all of our collections made from January to April. The species ranges from Mexico and the West Indies to northern South America.

*Iresine angustifolia* is recognized by the open much-branched inflorescences with flowers closely congested in quite separate pedunculate spikes, the broad lateral bracteoles twice as large as the basal bracts and equaling the perianth in length, the very narrow leaves both within and beneath the inflorescences, and the restriction to our seasonally dry Pacific lowlands. This species has been collected only a few times in Costa Rica in the areas around the Gulf of Nicoya and near the border with Nicaragua.

***Iresine arrecta*** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18:1550. 1938. Figure 30.

Clambering shrubs or woody lianas to 7 m high, apparently unisexual, leafy internodes 3.5–18 cm long, 1.5–7 mm thick, very minutely (0.2 mm) puberulent but soon becoming glabrous, longitudinally striate with usually more than 8 poorly defined longitudinal ridges, terete or obscurely 4-angled in cross section, nodes thickened in age and with an interpetiolar line or ridge. Leaves opposite or subopposite, petioles 6–30 mm long, 1–1.5 mm thick, broadly sulcate above with 2 adaxial ridges continuous with the lamina margins; laminae (4) 7–18 cm long, (1) 2–8.5 cm broad, ovate to ovate lanceolate, or lanceolate (and alternate) in the inflorescence, tapering gradually to the acute or less often acuminate apex, rounded and obtuse to subtruncate at the base, slightly decurrent on the petiole, margins entire, the laminae drying thin-chartaceous to chartaceous and smooth, very sparsely and minutely (0.2 mm) puberulent or glabrous, the midvein prominent above with 6–13 pairs of major secondary veins. Inflorescences terminal on the main axes or terminal on distal axillary shoots that often arise at right angles from the main stem, paniculate with numerous but distant glabrous or sparsely and minutely puberulent branches, to 30 cm long, the flowers in small (3–10 mm) sessile or very short-pedunculate spikes, bracts of the spikes and flowers sparsely puberulent, floral bracts 1–1.5 mm long, broadly ovate cuspidate, lustrous and translucent; male flowers with perianth 1.3–2 mm long, anthers ca. 0.5 mm long, elliptic, pistillode well developed but lacking stigmas; female flowers with perianth 1.2–1.6 mm long, ovary turbinate or obovoid, ca. 1 mm long, style very short with 2 long

(0.5 mm) stigmas. Fruit closely enclosed by the persisting perianth, subtended by tufts of villous or lanate whitish hairs 1–3 mm long arising from the base of the perianth abaxially; seed cochleate-orbicular, ca. 0.8 mm broad, lenticular in cross section, very dark brown and highly lustrous.

Rarely collected clambering or climbing plants of wet evergreen montane (premontane and lower montane rain) forest formations between 1,200 and 1,800 m elevation; flowering material has been collected from late November to early March. The species is known only from central Costa Rica.

*Iresine arrecta* is distinguished by its climbing habit, long slender petioles, thin leaves often rounded at the base and with numerous secondary veins, and separate little spikes of functionally unisexual sparsely puberulent flowers. The species is similar in some respects to *I. costaricensis* (q.v.) and *I. argentata* (Mart.) Dietr. of northern South America, but both of those species have densely sericeous inflorescence branches with bisexual flowers. Presently, *I. arrecta* is known only from near Zarcero, Alajuela (A. Smith A 617 and H 149, the type), near El Muñeco, Cartago (*Standley & Torres* 51090), and above San Isidro del General, (*Skutch* 2563).

***Iresine calea*** (Ibáñez) Standley, Contrib. U.S. Natl. Herb. 18:94. 1916. *Gomphrena latifolia* Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles 10, pt. 1:349. 1843. *Achyranthes calea* Ibáñez, *Naturaleza* 4:79. 1879. *I. latifolia* Benth. & Hook., Gen. Pl. 3:42. 1880, not Dietr. 1839. Figure 30.

Shrubs or clambering and vinelike, 1.5–4 (5) m tall, unisexual, leafy internodes 2.5–13 cm long, 1.5–5 mm thick, sparsely or more often densely short (0.2–0.5 mm) hirsutulous with whitish or very pale yellowish brown hairs, becoming glabrous and the nodes thickened, irregularly longitudinally striate when dry, the interpetiolar line or ridge usually obscure (sometimes absent). Leaves opposite, petioles 4–15 mm long, sulcate above with 2 adaxial ridges continuous with the lamina margins: laminae 1.5–8 (11) cm long, 1–4 (7) cm broad, ovate or occasionally ovate-lanceolate, tapering to an acute apex, usually rounded or obtuse at the base, margins entire and decurrent on the petiole, laminae drying chartaceous and smooth, usually densely hirsutulous or sericeous beneath with thin whitish hairs ca. 0.5 mm long and more sparsely puberulent above, midvein prominent above and with 4–8 pairs of major secondary veins. Inflorescence paniculate, 10–50 cm long, the open divergent branches densely puberulent, the spikes separate (2–10 mm) along the rachis and sessile or pedunculate, the male and female spikes quite different in appearance; male spikes with floral bracts ca. 0.5 mm long and clearly exceeded by the narrow perianth, the perianth parts 1.5–2 mm long, narrowly oblong, blunt and puberulent apically, often lustrous in the lower half abaxially, stamens united only at the base and not forming a conspicuous cup, pistillode usually slender and translucent; female spikes with the flowers hidden by much larger (1–1.5 mm) broadly ovate bracts, with dense tufts of tomentulous hairs from the bottom of the perianth further obscuring the flowers, perianth parts ca. 1.5 mm long and narrowly lanceolate, ovary ca. 0.7 mm long, style with 2 slender stigmas ca. 0.5 mm long. Fruit apparently tightly enclosed within the persisting perianth and bracts; seeds not seen.

Shrubs or clambering plants of low second growth and thickets from near sea level to 1,300 (1,800) m elevation on the Pacific slope and Central Mountains in Costa Rica; flowering in the dry season, from December through April. This species ranges from Mexico to the eastern edge of the Meseta Central in Costa Rica along the Pacific slope and Central Highlands of Central America.

*Iresine calea* is distinguished by its generally shrubby habit, dense whitish puberulence on young stems, undersides of leaves, and inflorescences, and the rather different bracts subtending the morphologically distinct male and female flowers. The different appearance of male and female spikes and the difficulty

of finding female flowers among bracts and hairs are also noteworthy. This species has not been collected from the Caribbean slope below 1,200 m elevation; it appears to prefer the seasonally dry habitats of the Pacific side of Central America and is especially common in the Meseta Central. Names applied to this species in central and southern Central America include: *Algodoncillo*, *Chivito*, *Chivo*, *Comenternero*, *Coyuntura*, *Flor de corona*, *Siete Pellejos*, and *Tacuquelite*.

*Iresine completa* Uline & Bray (Bot. Gaz. 21:349, 1896) was originally described from San Pedro Sula, Honduras, and is distinguished by its larger (2.5 mm) bisexual short-pedicellate flowers and narrow elliptic-lanceolate leaves glabrous on the upper surface except above the midrib. I have seen no authentic material of this species nor any specimens from our area which clearly fit the description. See the discussion by Duke in the Flora of Panama (Ann. Missouri Bot. Gard. 48:33, 1961). This species is related to *I. costaricensis* and *I. hassleriana* on the basis of the short thick stigmas.

***Iresine costaricensis* Standl., Contrib. U.S. Natl. Herb. 18:94. 1916. Figure 30.**

Clambering shrubs and lianas to 15 m high, bisexual, leafy internodes (1.5) 5–12 cm long, 2–6 mm thick, terete, densely sericeous with short (0.5 mm) appressed-ascending brownish hairs, becoming glabrescent and the nodes thickened, stems often becoming contracted above the node and interpetiolar line after drying. Leaves opposite, petioles 6–17 mm long, sulcate above, with adaxial ridges continuous with the lamina margins; laminae 7–18 cm long, 3–7.5 cm broad, elliptic-ovate, to elliptic-oblong or broadly elliptic, short-acuminate (in the type) to long-acuminate, with a narrow apex 4–10 mm long, obtuse at the base and decurrent on the petiole, entire but drying slightly undulate, the laminae drying stiffly chartaceous, and smooth, sparsely puberulent above and more densely below with thin straight appressed hairs ca. 0.5 mm long, with 7–12 pairs of major secondary veins. Inflorescences terminal on the main stem or on lateral branches, paniculate to 50 cm long and with strictly opposite branching, the flowers in small (3 mm thick) densely strigilose spikes or clusters, the flower cluster sessile or less often pedunculate, bracts at the base of the spike ca. 1 mm long, these and some of the floral bracts (ca. 0.5 mm) densely hirsutulous-strigilose, bracteoles subtending the flowers ca. 1 mm long and glabrous abaxially, very broadly ovate, tufts of long (1–2 mm) straight white hairs developing from the base of the flower within the bracteoles; flowers sessile, apparently bisexual, perianth parts ca. 1.5 mm long, oblong, obtuse at the apex, puberulent, filaments slender and united near the base to form a short cup, style very short with a thickly lobed stigma. Fruiting material not seen.

Rarely collected lianas or shrubs from wet evergreen montane forests and presently known only from the Caribbean slope at about 625 m elevation and above the General Valley at 1,800 m elevation; flowering material has been collected in December and March. The species is only known from central Costa Rica.

*Iresine costaricensis* is recognized by its stiff leaves with up to 12 pairs of major secondary veins, the inflorescences with consistently opposite divisions, young flower buds covered with a dense tomentum of pale yellowish brown hairs, and the short capitate stigmas. The very broad, almost glabrous bracteoles are usually only found with well-developed flowers. *Iresine costaricensis* was originally known only from two collections made by Adolfo Tonduz (12919 and 13183, the type) near Tucurrique, Cartago. These two collections appear to have been from woody climbing plants. A recent collection (*Burger & Liesner* 7057) from an erect shrub from above San Isidro del General is tentatively placed here. This latter collection has narrow elliptic-oblong leaves that are short-acuminate and the inflorescences, bracts, and perianth parts are not as puberulent as those in the



Tonduz collections. Both collections have the unusually short thick stigmas. This species is closely related to *I. hassleriana* Chodat, originally described from Paraguay. Our material has smaller perianth parts, a shorter staminal tube, and a shorter more rounded stigma than do the flowers of type material of *I. hassleriana* (Hassler 3429 F). The illustration of *I. hassleriana* in Flora of Panama is somewhat intermediate, but closer to the material from Paraguay. At present, it seems best to maintain *I. costaricensis* as a separate and distinct species closely related to *I. hassleriana*.

*Iresine diffusa* Humboldt & Bonpland ex Willd., Sp. Pl. ed. 4, 4:765. 1806, *Celosia paniculata* L., Sp. Pl. 1:206. 1753. *Iresine celosia* L., Syst. Veg. ed. 10, 1291. 1759, nomen illeg. *I. celosioides* L., Sp. Pl. ed. 2, 2:1456. 1763, nomen illeg. *I. paniculata* (L.) O. Ktze., Rev. Gen. 2:542. 1891, not *I. paniculata* Poir. Figure 30.

Herbs, subshrubs, or shrubs to 3 (5) m tall, unisexual, the rootstock and lower stem usually becoming woody, stems erect or clambering, leafy internodes 1–15 cm long 1–6 mm thick, occasionally glabrous but more often sparsely puberulent with short (0.1–0.5 mm) thin crooked hairs, internodes usually with 4 or 6 longitudinal ridges, the nodes slightly thickened below the leaf base and with an interpetiolar line or puberulent ridge, stems often narrowed just above the leaf bases when dried. Leaves opposite or subopposite, petioles 0.4–5 (8) cm long, sulcate above with 2 narrow adaxial ridges continuous with the lamina margins; laminae 2–16 cm long, 1–10 cm broad, elliptic ovate to broadly ovate or lanceolate (small and linear on the inflorescence), tapering gradually to an acuminate or acute apex, acute to obtuse or rounded at the base and decurrent on the petiole, margins entire, the laminae drying thin chartaceous and smooth to the touch, usually sparsely puberulent beneath with short (0.1–1 mm) thin hairs, the midvein prominent above with 3–9 pairs of major secondary veins arising at angles of 40°–70°. Inflorescences extremely variable in form and size, essentially terminal on the main or lateral axes, paniculate arrangements with the ultimate divisions made up of short spikes with 5–35 crowded flowers (becoming separate in fruit) the distal inflorescence branches usually alternate and often subtended by small lanceolate to linear leaves becoming short-linear or bractlike near the ultimate branches, the overall inflorescence from 5–50 cm long and whitish in color, the flowers subtended by subequal bracts and bracteoles 0.3–1 mm long, broadly ovate and concave, mucronate, translucent to pale yellowish or white; flowers sessile, unisexual, the perianth 0.7–1.5 mm long, stamens 5, united near the base to form a short tube, ovary obovoid, style very short with 2 (3) slender stigmas. Fruit loosely enclosed within the persisting perianth, long (1–2 mm) straight hairs sometimes formed between the bracts and the perianth; seeds cochleate-orbicular, lenticular in cross section, 0.5–0.8 mm long, very dark brown and lustrous.

Plants of secondary growth in open sunny or partially shaded sites in both very wet evergreen formations and, less commonly, in seasonally very dry deciduous formations from near sea level to 2,600 m elevation; in Costa Rica, some plants can probably be found in flower throughout the year, but almost all of our fertile collections have been made between October and May, with a great majority of the collections made in December, January, February, and March. The species ranges throughout the American tropics.

*Iresine diffusa*, formerly called *Iresine celosia*, is one of Costa Rica's most common and conspicuous weeds. The species is recognized by the usually large, white, many-branched paniculate inflorescences with very small unisexual white flowers, stems with longitudinal ridges and unusual nodes, and thin opposite leaves. The plants are most often collected in evergreen and partially deciduous formations below 1,500 m elevation. There is considerable variation regarding the size and arrangement of flowers and bracts in the material placed under this name. It may be that more than one specific entity is included under



the broad interpretation adopted here. Material previously placed under the name *I. acicullaris* Standl., *I. frutescence* Moq., and *I. spiculigera* Seub. is included here, following James Duke in the Flora of Panama (Ann. Missouri Bot. Gard. 48:35, 1961). Common names used in central and southern Central America include: *Adorno de niño*, *Camrón*, *Coyontura de pollos*, *Hierba de gato*, *Siete pellejos*, *Taba de gueguecho*, *Velo de gueguecho*, and *Velo de princesa*.

#### PF AFFIA Martius

REFERENCE: O. Stutzer, Die Gattung Pfaffia. Repert. Spec. Nov. Regni Veg. Beih. 88:1-46. 1935.

Herbs, shrubs, or climbers, densely puberulent to glabrescent, stems often with long internodes (in ours) and interpetiolar ridges or lines, often with a tuft of hairs in the leaf axil; stipules absent. Leaves opposite and simple, petiolate or sessile, entire and pinnately veined. Inflorescences varied, heads, fascicles, or solitary flowers often on opposing spike-like axes on terminal stems that bear reduced leaves forming compound panicles; flowers bisexual or sometimes reduced and nonfunctional, radially symmetrical, small and sessile, subtended by a bract and 2 lateral bracteoles, bract and bracteoles subequal, puberulent, flowers often with an unpleasant odor, greenish white, perianth of 5 subequal parts, often with 3 prominent longitudinal veins on the outer perianth parts, usually puberulent and with tufts of straight whitish hairs from the base within, persisting but not enlarging in fruit, stiff and dry, stamens 5, united below to form a short cup, the cup and filaments with or without appendages, anthers 2-theous, ovary ovoid to obovoid, 1-locular, with 1 ovule borne on an elongated funicle from a basal placenta, style very short and bearing a thick 2-lipped stigma. Fruit a thin-walled capsule (utricle), usually obscured by the persisting perianth, bracts, and tufts of hairs; seeds lenticular, reniform to cochleate-orbicular, reddish brown (in ours).

A poorly defined neotropical genus of probably fewer than 20 species, closely related to *Iresine* and *Gomphrena* and intermediate between them in some respects. The relatively few collections and their distribution in Costa Rica may indicate that our species has been introduced. Our plants are recognized by their clambering or climbing stems with long internodes and stiff opposite entire leaves and compound inflorescences with puberulent little flowers with a stiff dry perianth that bears tufts of whitish hairs from the base adaxially (between the perianth and the sexual parts). This species and other members of the genus are easily confused with species of *Iresine*, especially *I. arrecta* and *I. costaricensis*, in our flora.

**Pfaffia grandiflora** (Hook.) R. E. Fries, Ark. Bot. 16, no. 12:10. 1921. *Iresine grandiflora* Hooker, Icon. Pl. 2; tab. 102. 1837. *Gomphrena paniculata* var. *hookeriana* Seub., in Martius, Fl. Brasil. 5, pt. 1:192. 1875. *Hebanthe hookerianus* Hemsley, Biol. Cent. Amer. 3:19. 1882. *Pfaffia hookeriana* (Hemsl.) Greenman, Publ. Field Columbian Mus., Bot. Ser. 2:330. 1912. *P. hookeriana* forma *glabriuscula* Suesseng., Repert. Spec. Nov. Regni Veg. 35:332. 1934. Figure 27.

Woody climbers to 3 m long, leafy internodes 2-15 cm long, 1-5 mm thick, sparsely puberulent to glabrescent with slender ascending hairs 0.5-1.5 mm long, more densely puberulent at the nodes and in the leaf axils. Leaves opposite, petioles 3-15 mm long, with lateral margins often forming an adaxial sulcus in the lower half; laminae 3-12 cm long, 1.5-6 cm broad, ovate to lanceolate or elliptic, acute to acuminate at the apex, rounded to obtuse at the base, margin entire or slightly undulate, decurrent on the petiole, the laminae drying very stiffly chartaceous and pale or dark in color, smooth above and below, with stiff slender appressed (strigose) hairs on both surfaces, with 3-5 pairs of major secondary veins. Inflorescences usually compounded panicles at the ends of branches or

lateral stems, made up of spikelike axes 1–5 cm long, the axes often opposite and subtended by small leaves, the flowers usually solitary, sessile and subtended by a bract and 2 bracteoles 1–2 mm long and 1–2 mm broad at the base; flowers bisexual or nonfunctional, perianth of 5 subequal parts, 2–3.5 mm long, 1–2 mm broad, with short thin whitish hairs on the outer surface and thin silky hairs 3–8 mm long borne from the base of the inner surface, stamens 1.5–2.5 mm long, forming a short (0.5 mm) tube at the base and with anthers ca. 0.5 mm long; pistil with short style and broad 2-lobed stigma. Fruit a utricle ca. 2 mm long, included within the persisting perianth and bracts and obscured by the long thin whitish hairs from the interior of the perianth parts; seeds lenticular, reddish brown, ca. 1.5 mm broad.

Uncommon climbing or clambering plants of wet or seasonally dry evergreen formations and collected in flower and fruit in February, March, and April in Costa Rica. Most all of our collections come from between 900 and 1,400 m elevation around the Meseta Central with only a very few from lower areas. The species ranges from Mexico through Central America to Peru and the Guianas.

*Pfaffia grandiflora* is recognized by the clambering stems with opposite thin entire leaves, compound inflorescences with sessile flowers, and long silky hairs from within the perianth which obscure stamens, pistil, and fruit.

### PHILOXERUS R. Brown

Perennial herbs or subshrubs, prostrate, procumbent, or erect, bisexual, glabrous or puberulent; stipules absent. Leaves opposite and simple, sessile and often clasping the stem at their base, entire and pinnately veined, usually semisucculent. Inflorescences solitary, terminal or axillary, short- to long-pedunculate, often subtended by a pair of small leaves, the flowers sessile or subsessile and densely crowded in short spikes or capitula, flowers subtended by a bract and 2 bracteoles, the bract and bracteoles chartaceous and subequal; flowers bisexual and radially symmetrical, with 5 imbricate subequal perianth parts, the inner 2 usually narrower than the outer 3, acute at the apex, stamens 5, united near the base to form a very short tube, the tube lacking pseudostaminodial appendages, anthers 2-thecous, with introrse dehiscence, ovary with 1 locule and 1 ovule borne on a long funicle, style short and with 2 (3) stigmas. Fruit an orbiculate indehiscent utricle; seed lenticular to cochleate-orbicular, smooth, the embryo annular.

The genus is most distinctive among our Amaranthaceae, with its very narrow semisucculent leaves, short dense spikes, and prostrate habit near seashore environments. Here considered part of the genus *Philoxerus*, our species has been placed in the genus *Caraxeron* Vaillant ex Rafinesque by Mears (Taxon 29:88, 1980).

***Philoxerus vermicularis* (L.) R. Br., Prodr. 416. 1810. *Gomphrena vermicularis* L., Sp. Pl. 224. 1753. *Caraxeron vermicularis* (L.) Rafinesque, Fl. Telluriana 3:38. 1837. Figure 39.**

Semisucculent herbs from a woody base, usually procumbent or prostrate and sometimes forming loose mats, leafy internodes 1–8 cm long, 1–4 mm thick (dry), terete but becoming longitudinally ridged when dry, glabrous but with thin whitish hairs in the axils of the leaves, succulent and greenish in life. Leaves opposite and decussate, semisucculent, clearly differentiated from the stem at the base but not articulate, a petiole not clearly differentiated and the lamina narrowed to a clasping base; laminae (1) 2–5.5 (8) cm long, 2–8 (14) cm broad, linear to narrowly oblanceolate, usually broadest above the middle, rounded to obtuse at the apex but often with a small mucronate tip, gradually narrowed to the base, slightly expanded at the base and clasping the stem, margin entire, smooth and glabrous above and below, venation obscure. Inflorescences solitary and terminal or less often axillary, short-spicate to capitate, usually very short (0.5–1 cm) pedunculate above a reduced pair of foliage leaves, flowering portion of the spike 6–18 (28) mm long, 8–10 mm thick, rachis obscured by the flowers and bracts but with thin whitish

hairs, flowers sessile or subsessile, subtended by a short (1 mm) abaxial bract and 2 lateral narrow bracteoles ca. 2 mm long; flowers with the perianth 3–3.5 mm long, dull white in life and becoming pale straw colored when dry.

A species of sandy and rocky seashores on both the Pacific and Caribbean shores of Central America; probably flowering throughout the year in our area. The species ranges from Florida, Texas, and Mexico, through Central America and the West Indies to Ecuador and Brazil; this species is also found on the west coast of Africa.

*Philoxerus vermicularis* is immediately distinguished by its seaside habitat, succulent prostrate stems, very narrow opposite leaves, and dense spikes with scarious whitish bracts. These plants appear to be quite uncommon on the beaches of Central America. Only three collections are known from our area: *Pittier* 12692 from Puerto Limon, *J. Leon* 494 from Caldera, Puntarenas, and *von Wedel* 1948 from Bocas del Toro, Panama.

### PLEUROPETALUM Hooker f.

Herbs or shrubs, the stems sometimes climbing, plants bisexual, stems glabrous or sparsely and minutely puberulent and becoming glabrous; stipules absent. Leaves alternate in a spiral or occasionally distichous, simple and petiolate, pinnately veined, thin in texture. Inflorescences mostly solitary, terminal or axillary, racemes or compound paniculate arrangements usually made up of racemose branches and often with reduced foliage leaves, glabrous or minutely puberulent; flowers bisexual and radially symmetrical, pedicellate to subsessile, subtended by 1 bract and 2 bracteoles, these often close together beneath the perianth and simulating a second smaller perianth whorl, the bracts and perianth parts often with the same stiff texture and color, perianth of 1 whorl of 5 free oblong somewhat concave subequal sepals (tepals), imbricate in bud, stiff and persisting in fruit but not enlarging, green to yellowish or red in fruit, stamens 5–8, united near the base to form a short filament-tube or cup, free portion of the filaments slightly flattened, anthers 4-theous, pistil 1, ovary subglobose, 1-locular with many ovules on slender stalks from a central basal placenta, style 1 and very short with 3–8 small stigmas. Fruit at first slightly succulent and berry-like but becoming dry and capsule-like, opening irregularly or with circumscissile dehiscence in the lower half, subtended by the stiff perianth parts; seeds laterally flattened and somewhat lenticular, cochleate-orbicular to reniform-orbicular in outline, borne on slender funicles, the testa lustrous black; embryo annular.

A neotropical genus of perhaps three species ranging from central Mexico to Peru and with an endemic species on the Galapagos Islands. These plants are distinguished by their thin leaves on slender petioles, the flowers with what appear to be two whorls of stiff straw-colored (dry) perianth parts, the stamens forming a short cup at their base, the slightly fleshy capsule-like fruit that often opens around the middle or lower half, and the shiny black seeds borne on slender stalks from a basal placenta. The distinctive perianth becomes very stiff when dry, pale yellowish brown and with many longitudinal ridges, resembling the glumes of grasses.

- 1a Seeds 1.5–2.5 mm long, larger perianth parts usually 3–4 mm long, inflorescence a compact panicle with rounded contours; plants erect and few-branched, 500–1,900 m  
*P. sprucei*
- 1b Seeds 1–1.5 mm long, larger perianth parts usually 4–5 mm long, inflorescences open racemes or open panicles with racemose branches; plants often climbing or clambering over others, 0–900 m elevation.....*P. pleiogynum*

**Pleuropetalum pleiogynum** (O. Ktze.) Standley, J. Wash. Acad. Sci. 13:369. 1923. *Celosia pleiogyna* O. Kuntze, Rev. Gen. 541. 1891. *P. standleyi* Suessenguth, Rept. Spec. Nov. Regni Veg. 44:41. 1938. Figure 29.



Shrubs, erect or arching over other plants, to 3 m tall or climbing to 5 m high, leafy internodes 2–6 cm long, 1–4 mm thick, glabrous, weakly longitudinally ridged. Leaves alternate in a spiral, glabrous, petioles 0.6–2 (4) cm long, about 1 mm thick, with a narrow adaxial sulcus in the basal half, decurrent on the stem; laminae (3) 5–15 cm long (1) 2–5 cm broad, elliptic-ovate to narrowly elliptic, narrowly elliptic-oblong or lanceolate, gradually narrowed to the acuminate (acute) apex, attenuate at the base, margins entire and decurrent on the petiole, the laminae drying chartaceous and usually dark in color, smooth and glabrous on both surfaces, with (3) 4–6 (8) pairs of major secondary veins. Inflorescences racemes or panicles of racemes, axillary or terminal, to 30 cm long, the individual racemes 1–6 cm long, the rachis often with a zigzag form, glabrous or very minutely puberulent, pedicels 0.5–2 mm long, becoming 5 mm long in fruit, subtended by an ovate bract 1–2 mm long with thin membranous edges; flowers ca. 4–6 mm long, subtended by short (2 mm) broad-based bracteoles, perianth ca. 4 mm long, with usually more than 20 longitudinal ribs, pale yellow to red, ovary usually with 5 or 6 stigmas. Fruit a capsule 5–7 mm long, opening by circumscissile dehiscence, upper part cream and the lower part orange in color; seeds 1–1.5 mm long, lustrous black, usually more than 30 per capsule.

Plants of forest edges and stream sides in wet evergreen formations from near sea level to 900 m elevation, but only rarely found above 500 m in Costa Rica; flowering and fruiting collections have been made mostly between August and April. The species ranges from western Costa Rica to central Panama.

*Pleuropetalum pleiogynum* is recognized by the open racemes or panicles of flowers with stiff persisting perianth parts, the many longitudinal ridges on the perianth, and the circumscissile dehiscence of the slightly succulent capsule. The arching, clambering, or climbing stems in partly open sites further distinguish this species.

***Pleuropetalum sprucei*** (Hook. f.) Standl., N. Amer. Fl. 21:96. 1917. *Melanocarpum sprucei* Hook. f., in Benth. & Hook., Gen. Pl. 3:24. 1880. *P. costaricense* nom. nud., in Hemsl., Biol. Centr. Am. Bot. 3:12. 1882. *P. costaricense* Wendl. ex Hook. f., Bot. Mag. pl. 6674. 1883. *P. tucurriquense* Donn. Sm., Bot. Gaz. 61:387. 1916. *P. calospermum* Standl., J. Wash. Acad. Sci. 13:368. 1923. Figure 29.

Small shrubs, (0.5) 1–2 (3) m tall, few-branched and erect, leafy internodes 0.5–5 cm long, 1.2–6 mm thick, glabrous or minutely and very sparsely puberulent, becoming longitudinally ridged. Leaves alternate in a spiral, petioles 1–4 (6) cm long, ca. 1.5 mm broad, with 2 adaxial ridges producing a slight sulcus above, short-decurrent on the stem; laminae 5–20 (28) cm long, 2–8 (12) cm broad, elliptic to elliptic-oblong or narrowly elliptic-ovate to lanceolate, tapering gradually to the acuminate apex, tapering gradually to the attenuate base, margin entire and decurrent on the petiole, the laminae drying thin chartaceous and usually dark in color, smooth and glabrous above and below or with a few minute strigillose hairs along the veins, with 7–10 pairs of major secondary veins. Inflorescences terminal or axillary, solitary, usually compact panicles of short racemose branches, often somewhat flat-topped or a tight convex group (corymbose), 3–9 cm long, peduncles 1–4 cm long, secondary peduncles and rachis minutely (0.1 mm) and densely brownish puberulent, pedicels subtended by broad-based bracts ca. 1 mm long, pedicels 1–4 mm long, 2 or 3 small bracteoles usually subtending the flower just beneath the perianth; flowers ca. 4 mm long, perianth of a single whorl but appearing as 2 whorls because of the subtending bracteoles, perianth parts free, ca. 3 mm long and 1–1.5 mm broad, with usually fewer than 20 longitudinal ribs (striations), yellowish green to reddish at the base, fleshy in life, stamens ca. 2.5 mm long, ovary with usually 3 or 4 stigmas. Fruit ca. 6 mm long and 5 mm thick, becoming reddish to dark purple, dehiscing irregularly or circumscissile in the lower half; seeds 1.5–2.2 mm long, usually fewer than 30 per capsule.

Plants of shaded evergreen forest formations from 500 to 1,900 m elevation on both the Caribbean and Pacific slopes in Costa Rica; probably flowering and fruiting throughout the year, but with very few collections made in May and



June and in October and November. The species ranges from central Mexico to Peru.

*Pleuropetalum sprucei* is characterized by its usually short erect habit, flowers usually borne in small dense corymb-like panicles, and relatively large seeds. The persisting perianth that dries stiff and with many longitudinal ribs and is subtended by two or three small bracteoles with similar texture is quite distinctive.

## NYCTAGINACEAE

Herbs, shrubs or trees, erect or scandent, bisexual or unisexual, glabrous or puberulent, with or without spines, sometimes with viscid hairs, the nodes often somewhat thickened, often with dichotomous branching; stipules absent. Leaves alternate, subopposite, opposite or whorled, simple, petiolate, laminae entire and often with short-linear raphides visible as projections on the dried surfaces. Inflorescences solitary or several, terminal or axillary, variously branched but usually with the distal flowers in cymose groupings, with 1–3 bracts or bracteoles subtending each flower, these sometimes resembling a perianth whorl; flowers bisexual or functionally unisexual, radially symmetrical (in ours), with 1 perianth whorl but often appearing to have 2 whorls because of the sepaloid or petaloid bracts (as in *Bougainvillea*) or because of the differentiation between lower sepaloid and upper corolla-like parts of the perianth (as in *Boerhavia*), perianth united to form a broadly campanulate, urceolate to narrowly cylindrical tube, 5-lobed (rarely 3- to 7-lobed) at the apex or with 5 (3–7) small teeth, involute-plicate in bud or the lobes valvate, base of the perianth persisting in fruit, distal portion of the perianth persisting or deciduous; stamens 1–10 (many), filaments usually unequal in length and united at the base to form a short tube or united to the base of the pistil, anthers dorsifixed near the base, included within the perianth or exerted at anthesis; pistil solitary, often narrowed near the base or stipitate, ovary with 1 locule and 1 basal stalked ovule, style long to short or absent, stigma solitary, globose to fimbriate. Fruit usually enclosed within the persisting and protective perianth to form what is called an anthocarp, becoming fleshy, coriaceous or woody, the fruit a thin-walled nut that is not usually separable from the enclosing perianth; embryo strongly curved.

A family of tropical and subtropical plants with most of its species and genera found in the New World. The flowers and their bracts differ greatly in different genera, and they are often difficult to recognize as members of the same family. The perianth tube that is persistent and adherent around the fruit, the often stipitate ovary with single basal ovule and solitary stigma, the stamens united at the base to form a short tube, and the occasional elaboration of bracts to resemble either calyx or corolla are helpful in recognizing this family. The stalked basal ovule that produces a strongly curved or folded embryo are important features shared by other members of the Centrospermae (Caryophyllales). Except for a few important ornamentals, the family is of no economic importance; a number of species have become pantropical weeds.

Two genera of small weedy species with opposite leaves (*Allionia* with lenticular fruit and dentate winglike margins and *Commicarpus* with terete fruit with longitudinal ranks of stipitate glands) are known from Mexico and Guatemala and in South America, but have never been reported or collected in the regions between these areas.

*Cephalotomandra fragrans* Karsten and Triana (including *C. panamensis* Standley) looks very much like some of our larger leaved specimens of *Neea*. However, in *Cephalotomandra*, the male perianth forms an open cup and there are more than 20 stamens in each male flower. The genus is not known from Costa Rica, and considerable doubt exists that a specimen with a collection label from Panama

was actually collected in Panama (see Woodson's treatment in Ann. Missouri Bot. Gard. 48:55–56, 1961).

#### KEY TO THE GENERA OF NYCTAGINACEAE

- 1a Leaves alternate along the stem, none opposite .....2a
- 1b Leaves opposite along the stem, a few subopposite or alternate leaves occasionally present .....3a
- 2a Herbs, erect; flowers subtended by small green bracts; uncommon lowland plants  
*Salpianthus*
- 2b Woody climbers or shrublike; tubular flowers attached to broad brilliantly colored red, purple, or orange bracts, usually in groups of 3; widely planted for ornament  
*Bougainvillea*
- 3a Herbs, woody only at the base .....4a
- 3b Trees, shrubs or subshrubs .....5a
- 4a Bracts subtending the flowers inconspicuous; perianth tube with a distinctly differentiated calyx-like base and corolla-like upper portion, the perianth 1.5–5 mm long .....*Boerhavia*
- 4b Bracts united near the base of the flower to form a 5-parted calyx-like whorl; perianth tube 1–5 cm long, uniformly corolla-like and brightly colored  
*Mirabilis*
- 5a Stems frequently armed with spines (but not all stems have spines); small shrubs, trees, climbers or woody lianas; fruit often borne on very long stalks, with longitudinal ranks of viscid-tipped glands .....*Pisonia*
- 5b Stems never with spines; small shrubs or trees but not climbers; fruit sessile or stalked, lacking stalked viscid glands .....6a
- 6a Male flowers campanulate with the stamens well exerted from the broad perianth opening, female flowers with the stigmas exerted at anthesis and the pistil borne on a short stalk; fruit becoming dark purple or black, longitudinally ridged when dry; laminae rarely more than 15 cm long, drying dark in color; small to large trees (rarely shrubs); evergreen forests of the Pacific slope including the Nicoya peninsula, Meseta Central, General Valley, and Talamanca mountains, 0–2,000 m elevation... *Guapira*
- 6b Male flowers tubular to ellipsoid, the stamens included within the perianth tube, female flowers with the stigmas only rarely exerted, pistil sessile or narrowed at the base; fruit becoming yellow, orange or purple, occasionally longitudinally striate when dry; laminae to 30 cm long, drying pale or dark; small subshrubs to small trees (rarely more than 8 m tall); from the highlands and deciduous formations of northern Costa Rica to the western edge of the Meseta Central, common in the Caribbean lowlands and less so on the Caribbean slope and Osa Peninsula (apparently absent on the Talamanca mountains and in the General Valley), 0–1,600 m elevation ... *Neea*

#### BOERHAVIA Linnaeus

Herbs, annual or perennial, often with a woody base, bisexual, erect or prostrate, often much branched, stems often with viscidous areas on the internodes, gland-tipped hairs often present. Leaves opposite or subopposite, opposing leaves of a pair often very unequal, petiolate, entire or sinuate, raphides often visible as surface irregularities when dried. Inflorescences terminal, paniculiform to racemeiform with the flowers in small umbellate, cymose, capitate or racemose arrangements (rarely solitary), 1–3 slender bracteoles present beneath each flower. Flowers bisexual, radially symmetrical and very small, perianth of a single whorl united to form a calyx-like base and a thinner petal-like distal limb that is shallowly 5-lobed, the upper and lower areas of the perianth tube divided by a constriction, stamens 1–5, filaments slender and united at the base to form a very short tube or cup, pistil stipitate, ovary unilocular, style slender, stigma peltate or capitate, usually exerted. Fruit an anthocarp formed by the tight enclosure of the ovary within the perianth tube, obovoid to obpyramidal, 3–5 angled (rarely winged), glabrous or glandular-puberulent.

A genus of weedy plants ranging widely over the tropics and subtropics. Their

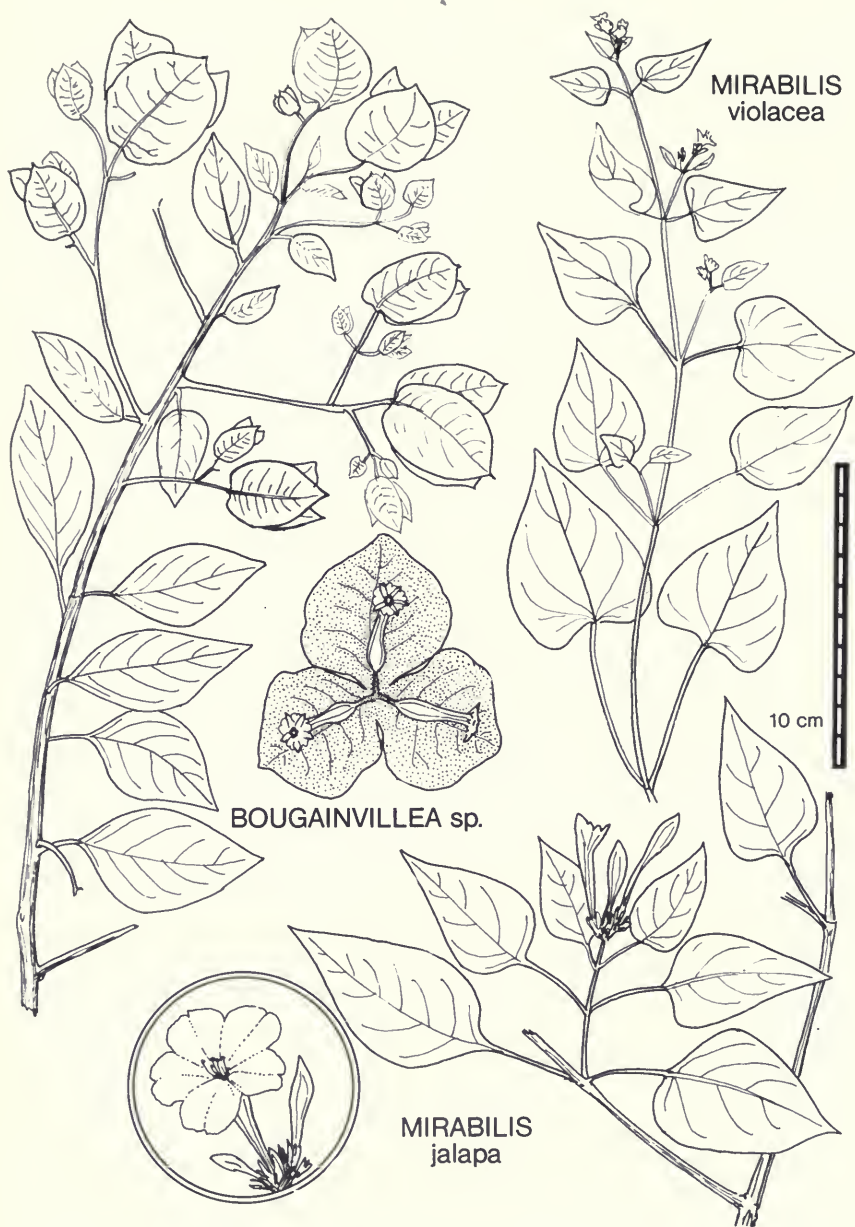


FIG. 31. Nyctaginaceae: a cultivated form of *Bougainvillea* and two species of *Mirabilis*.

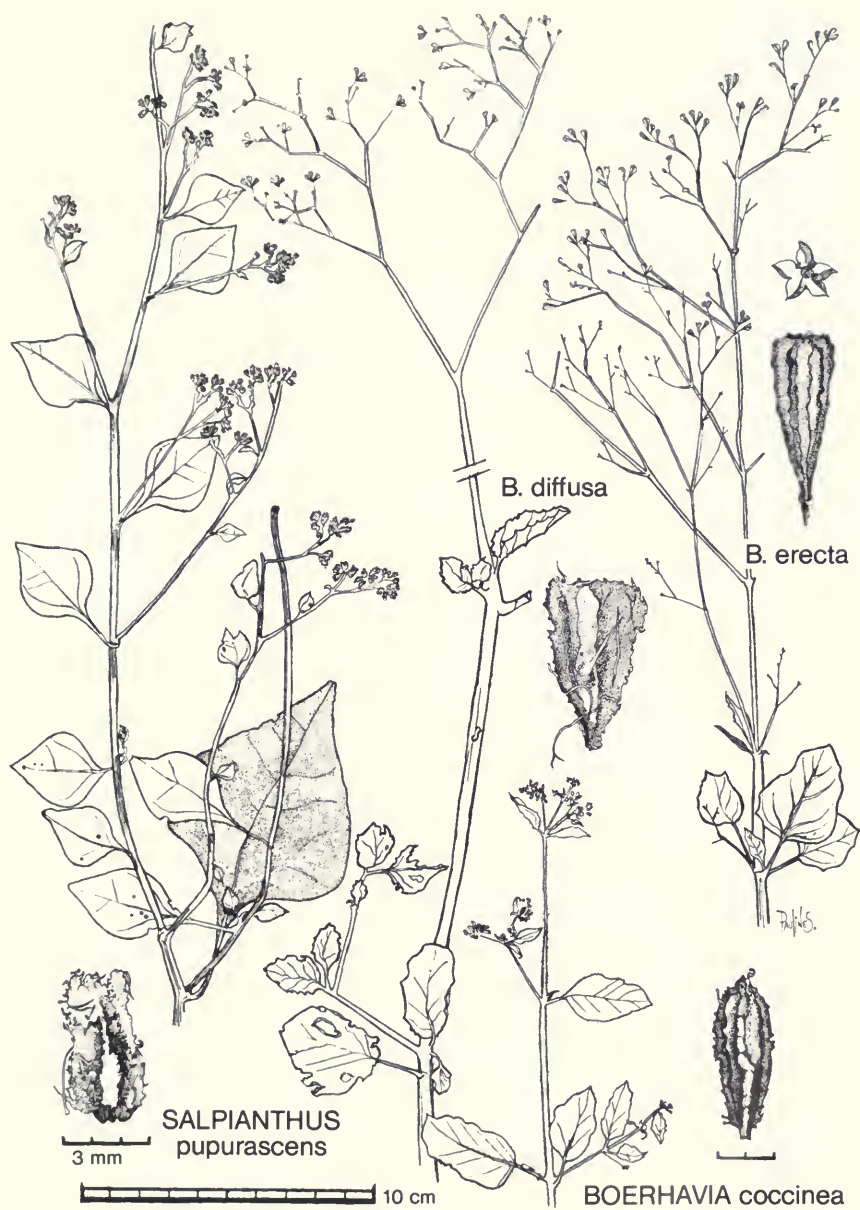


FIG. 32. Nyctaginaceae: three species of *Boerhavia* and a species of *Salpianthus*.





FIG. 33. Nyctaginaceae: a species of *Guapira* and two species of *Pisonia*. Note the different leaf form and habit in *P. aculeata*.



FIG. 34. Nyctaginaceae: Cost Rican representatives of the *Neea psychotrioides* species-group. These are part of a polymorphic assemblage that may not be reducible to species.



FIG. 35. Nyctaginaceae: Costa Rican representatives of the *Neea amplifolia* species-group. These are part of a polymorphic assemblage that may not be reducible to species.

distribution patterns in Costa Rica give the impression that these plants are not native elements of the flora. The genus is recognized by its opposite to subopposite leaves which often are very different in size at the same node, the frequent presence of gland-tipped hairs or viscous areas on the internodes, the perianth tube that is calyx-like beneath and corolla-like distally, slender filaments united at the base, capitate stigma and fruit resembling an inferior ovary and broadest near the apex. The following key and species concepts are based on the treatment of C. D. Adams in the Flowering Plants of Jamaica (1972, pp. 260–261).

- 1a Fruit glabrous and not at all viscid; distal perianth white to pink or lavender; stems and leaves minutely puberulent or glabrous, the internodes often with glutinous patches and the leaves usually pellucid-punctate beneath; inflorescence with many vertical branches and usually lacking leafy bracts; erect plants from a woody rootstock *B. erecta*
- 1b Fruit minutely viscid puberulent; distal perianth red to dark purple; stems and leaves minutely puberulent to densely viscid, lacking glutinous patches on the internodes and pellucid dots on the laminae beneath; inflorescence with spreading branches and usually with leafy bracts; decumbent to ascending plants ..... 2a
- 2a Flowers in distal clusters of 3–12, the inflorescences usually small and few branched, leaves and stems usually densely viscid puberulent ..... *B. coccinea*
- 2b Flowers in distal clusters of 2–5, the inflorescences often large and much branched; leaves and stems often with minute (0.1 mm) and longer (to 1 mm) thin hairs, not densely viscid puberulent ..... *B. diffusa*

**Boerhavia coccinea** Miller, Gard. Dictionary ed. 8, *Boerhavia* no. 4. 1768. *B. caribaea* Jacq., Obs. Bot. 4:5. 1771.

Decumbent or clambering herbs from a strong rootstock, to 0.8 m tall or ca. 1.2 m long, leafy internodes 2–12 (15) cm long, 1–5 (8) mm thick (dry), usually densely puberulent with slender viscid multicellular hairs 0.2–0.8 mm long. Leaves opposite and subequal, petioles 2–40 mm long, usually densely viscid puberulent; laminae 1.5–5 cm long, 0.7–3.5 cm broad, ovate to ovate-rhomboid or suborbicular, bluntly acute to obtuse or rounded at the apex, obtuse to cuneate or truncate and rounded at the base, margin entire or slightly sinuate (undulate), laminae drying thin- to stiff-chartaceous, and usually dark in color on the upper surface (dry), obscurely and very minutely (0.1 mm) to densely and conspicuously viscid puberulent (occasionally almost glabrous), with 3–5 major pairs of secondary veins. Inflorescences terminal on short lateral branches or terminal on the many-branched and leafy apex of the plant, flowers in small (3–10 mm broad) clusters of 3–12 on slender ultimate peduncles 3–15 mm long, glabrous to densely viscid puberulent. Flowers 2–3 mm long, rose-purple to deep red or red-purple, stamens 2, anthers ca. 0.3 mm long. Fruit 3–4 mm long, narrowly obovoid, ca. 1 mm thick at the thickest part, with 5 prominent longitudinal ribs, surfaces very minutely (0.1 mm) viscid puberulent.

Herbs of recently disturbed or open sandy sites in the lowlands of both the Caribbean and Pacific coastal plains, ranging to 600 m elevation in northern Central America; probably flowering throughout the year, but fertile collections have been made only from June to August and from November to February in our areas. The species ranges throughout the American tropics to Africa and Asia.

*Boerhavia coccinea* is recognized by the small brightly colored flowers tightly clustered in small groups of usually 4–10, the very short viscid pubescence on the fruit and usually on other plant parts as well, and the decumbent growth habit. These plants are frequently found near the seashore and in disturbed sites; their present distribution in Costa Rica makes it appear that they were not a native element of the flora. These plants are often placed under *B. diffusa*.



**Boerhavia diffusa** L., Sp. Pl. 3. 1753. *B. paniculata* L. Rich., Actes Soc. Hist. Nat. Paris 1:105. 1792.

Herbs to ca. 1 m tall, prostrate, decumbent or short-ascending, usually much-branched, leafy internodes to 20 cm long, sparsely puberulent with very small (0.1 mm) hairs and longer slender multicellular hairs to 1 mm long, often becoming glabrous. Leaves opposite, opposing leaves of the same node very different in size, small leaves on short axillary shoots often present at the widely separate nodes, petioles 3–15 mm long; laminae 1.5–6 cm long, 1–5 cm broad, ovate to ovate-oblong or ovate-rhomboid, bluntly obtuse to rounded at the apex, obtuse to truncate and rounded at the base, margin undulate-sinuate, drying chartaceous and with the lower surface often much paler in color than the upper surface, sparsely and minutely puberulent on both surfaces or with scattered longer hairs to 1 mm long, often puberulent along the edge, with 3–5 pairs of major secondary veins. Inflorescences on the open and diffusely branching terminal stems of the plant, small (1 cm or less) leaflike bracts subtending the major inflorescence branches, ultimate peduncles with 1–5 flowers, very variable in length, glabrous to minutely puberulent. Flowers ca. 2 mm long, pinkish to deep red or purplish in color. Fruit 3.5–4 mm long, narrowly obovoid to narrowly obtriangular, thickest (1 mm) near the apex, with 5 prominent longitudinal ridges, minutely (0.2 mm) viscid puberulent.

Plants of open recently disturbed weedy sites and sandy or gravelly situations in open sun on both the Caribbean and Pacific sides of Costa Rica from sea level to 1,200 m elevation; probably flowering throughout the year (no fertile collections have been made in May, September, October, or December in our area). The species ranges throughout the American tropics.

*Boerhavia diffusa* is recognized by the small clusters of red flowers on an open diffusely branched inflorescence, small viscid fruit thickest near the apex, leaves of very different size at the same node (both cauline leaves and those of axillary shoots), and the short stature. Often found along the sides of roads, in vacant lots in towns, and near the ocean shore, these plants give the impression of being recent arrivals in Costa Rica. This species is very closely related to *B. coccinea*, and it may be that the two are conspecific, but they seem to segregate themselves quite clearly in our area.

**Boerhavia erecta** L., Sp. Pl. 3. 1753.

Herbs 0.3–1.2 m tall, erect, woody at the base, leafy internodes 2–15 cm long, 2–5 (8) mm thick, very minutely (0.1 mm) puberulent or becoming glabrous, occasionally with a viscid area on the internode, nodes with an interpetiolar line or ridge. Leaves opposite, petioles 2–40 (60) mm long, very minutely puberulent; laminae 1–5 (8) cm long, 0.5–5 (7) cm broad, ovate to broadly elliptic or triangular, obtuse to bluntly acute at the apex, abruptly obtuse to truncate or rounded at the base, margin irregularly sinuate, smooth, sparsely and very minutely puberulent on both surfaces, drying much paler in color beneath, dark glandular dots often present on one or both surfaces, with 3–5 pairs of major secondary veins. Inflorescences to 40 cm long, with many slender (0.5 mm dry) opposite branches, the flowers variously arranged in groups of 2–5, sessile or sometimes an individual flower on a slender pedicel, inflorescence branches and pedicels glabrous or obscurely (0.05 mm) puberulent; floral bracts ca. 1 mm long, linear-lanceolate. Flowers 1.5–2.2 mm long, with a greenish calyx-like base ca. 1 mm long and a thin corolla-like distal portion 0.8–1.2 mm long, pale greenish white to white tinged with pink or pale lavender. Fruit narrowly obpyramidal, 3–4 mm long and 1.3 mm broad at the apex, tapering gradually to the narrow base, strongly 5-angled in cross section with 5 longitudinal ridges and grooves, essentially glabrous.

Weedy plants of open early secondary vegetation in both seasonally very dry areas and in evergreen formations from just behind the ocean shore to 600 (rarely to 1,200) m elevation; probably flowering throughout the year, but with most collections having been made between February and August in Costa Rica.

Widespread in the tropics and subtropics of the Western Hemisphere and in Africa.

*Boerhavia erecta* is recognized by the distinctive little glabrous fruit, the diffuse many-branched inflorescence (in larger specimens), the opposite leaves often unequal at a node and with irregular outline, and the little flower with a perianth tube that appears to be divided into calyx and corolla. The viscid areas on the stems and the gland dots on the leaves are also noteworthy, but not always apparent. This species is very common in our Pacific lowlands, but uncommon in the Caribbean lowlands where it has been collected only in the general vicinity of Limon.

### BOUGAINVILLEA Commerson

REFERENCE: W. T. Gillis, *Bougainvilleas of cultivation*. *Baileya* 20:34–41. 1976.

Woody vines, sometimes forming shrubs or small trees, bisexual, glabrous or puberulent, stems often armed with short spines. Leaves alternate and petiolate, laminae entire and pinnately veined. Inflorescences solitary, borne on modified axillary shoots, usually consisting of a group of 3 flowers, each flower subtended by a large leaflike bract, the pedicel of the flower adnate to the midrib of the bract on the inner (adaxial) side and the bracts surrounding the flowers, the bracts usually 2–4.5 cm long and brilliantly colored. Flowers bisexual and radially symmetrical, perianth of a single whorl united to form a long narrow tube with a small star-shaped distal 5-lobed limb, perianth tube terete or 5-angled, yellowish to whitish or less often the same color as the bracts; stamens 8–10, filaments slender and unequal in length, united near the base, anthers included in the tube or a few exerted; pistil borne on a short stalk, ovary narrowly ellipsoid and unilocular, ovule solitary, style straight or curved, stigma long and papillose, included within the perianth tube. Fruit an anthocarp formed by the perianth tube tightly enclosing the fruit and seed, narrowly ellipsoid, with 5 longitudinal ribs.

A genus of probably 10 to 15 species native to central and southern South America. These plants are recognized by their woody usually climbing stems, alternate entire leaves, and brilliantly colored leaflike bracts in groups of three that include three narrowly tubular flowers. The brilliant bracts which remain colorful for months and the woody climbing habit which allows the plants to be grown in a variety of forms over various supports have made these plants important ornamentals in frost-free areas. The plants rarely set seed and are propagated vegetatively. Because of their popularity, they are known by a variety of names: *Bogambilla*, *Bombilla*, *Bugambilla*, *Buguenvitia*, *Flor de Verano*, *Lustrosa*, *Manto de Jesús*, *Napoleón*, *Pomonce*, *Pompilla*, *Primavera*, *Santa Rita*, *Sempre Lustrosa*, *Tres Marias*, *Trinitaria*, and *Veranera*.

These plants are not known as escapes in our area, and because of propagation by vegetative means, it is difficult to establish species limits. Species descriptions are not provided here (see fig. 31), but the following key, based on Gillis 1976, should be helpful. For a thorough discussion of the cultivars, see L. H. MacDaniels' article on this subject in *Baileya* 21:77–100, 1981.

- 1a Perianth tube distinctly angled with longitudinal ribs and with spreading straight hairs to 1 mm long; stems and leaves villous; rare in Central America  
*B. spectabilis* Willd.
- 1b Perianth tube with distinct longitudinal ribs and with upward curving hairs to 0.5 mm long; stems and leaves glabrous to puberulent; commonly planted in Central America ..... 2a
- 2a Leaves broadly ovate, becoming smaller below the inflorescence; bracts deep red or orange and with obtuse apices, not crinkled; flowers closely grouped; stems with straight thorns ..... *B. buttiana* Holtum and Standley

- 2b Leaves narrowly ovate to elliptic, not becoming smaller below the inflorescence; bracts magenta to purple and with acute apices, often crinkled; flowers usually separate; stems with curved thorns or thorns absent ..... *B. glabra* Choisy in DC.

### GUAPIRA Aublet

Trees and shrubs, functionally unisexual (dioecious), puberulent in early stages but often becoming glabrous. Leaves opposite, whorled or occasionally subopposite, often very variable in size on the same plant or at the same node, petiolate, entire, pinnately veined. Inflorescences terminal, 1–3, with a single primary peduncle and rachis and opposite or subopposite branching, densely and minutely brownish or reddish puberulent, becoming succulent in fruit, flowers usually in groups of 2 or 3 on the ultimate inflorescence branches, and subtended by 1–3 minute bracts. Male flowers obconic, to campanulate or funnel-shaped, the 5 small distal lobes valvate in bud, green to white or yellowish, stamens usually 8 (5–10), filaments slender and unequal, united at the base to the stipe of the pistillode, anthers versatile and exerted well beyond the floral cup. Female flowers tubular to tubular-campanulate, staminodes with large sterile anthers and included within the perianth tube, pistil narrowly ovoid and with a basal stipe adnate to the filament tube, locule 1, style 1, stigma penicillate or fimbriate. Fruit an anthocarp formed by enclosure of the ovary within the succulent perianth tube, drupaceous, the free distal portion of the perianth tube usually persisting (in ours), becoming red or black, longitudinally striate when dry.

A genus of perhaps 50 species ranging from Mexico through Central America and the West Indies to northern South America, Brazil, Paraguay, and Bolivia (apparently absent along the Pacific side of South America). These plants are recognized by their opposite or whorled leaves, terminal inflorescences with small flowers that appear to be bisexual but are functionally unisexual, perianth tube subtended by one to three minute bracts, exerted stamens and stigma, and drupaceous fruit that may appear to be the product of an inferior ovary. These plants resemble certain members of the Rubiaceae family, but lack stipules, two perianth whorls, and an inferior ovary. The genus *Torrubia* has been united with *Guapira*, and it is more than likely that *Neea* should also be submerged under *Guapira*.

We have very few collections of this genus from Costa Rica. While our material appears to represent a single species, there is some question if it is specifically distinct from *G. linearibracteata* (Heimerl) Standley of northern Central America and Mexico (with smaller leaves but larger flowers) and *G. standleyanum* as interpreted by Croat in the Flora of Barro Colorado Island (said to grow to 35 m in height and with puberulent fruit). Considering the perplexing variability in our material of *Neea*, it would not be surprising to find similar problems in *Guapira*.

***Guapira costaricana*** (Standl.) Woodson, Ann. Missouri Bot. Gard. 48:62. 1961. *Torrubia costaricana* Standley, Contr. U.S. Nat. Herb. 13:385. 1911.

Small trees 5–10 m tall (rarely shrubs), unisexual, leafy internodes 1–5 (8) cm long, 1.3–4 mm thick with slender brownish multicellular hairs, stems quickly becoming glabrous and pale grayish in age, little or obscurely lenticellate. Leaves opposite and subequal to very unequal at a node, often with a whorl of 4 leaves at flowering or branching nodes, usually drying dark in color, petioles 5–15 (25) mm long, with 2 lateral or adaxial ridges continuous with the laminae margins; laminae 4–15 (18) cm long, 2–6 cm broad, narrowly elliptic to elliptic or elliptic-oblong, (occasionally ovate to obovate in the short leaves) tapering to an acute or short-acuminate apex, acute to obtuse at the base (rounded at the base on the broad little laminae), entire, smooth on both surfaces, glabrous or becoming glabrous above and below, drying thin-chartaceous, with 6–10 pairs of major secondary veins, the venation often somewhat obscure. Male inflorescences 5–10 cm long, primary peduncle



2–6 cm long, peduncle and inflorescence branches minutely brownish puberulent, male flowers sessile or subsessile, subtended by minute (0.5 mm) bracts, floral cup 2–3 mm long and 2–3 mm broad at the campanulate apex (dry), filaments unequal, anthers ca. 0.6 mm long and exerted up to 3 mm beyond the perianth. Female inflorescences to 15 cm long in fruit, becoming red in color, minutely puberulent; female flowers 2–3 mm long, tubular, subtended by minute (0.5 mm) bracts, stigmas exerted 0.5–1 mm at anthesis. Fruit becoming broadly ellipsoid to subglobose, 8 mm long and 5 mm thick (dry), becoming dark purple or black, with obscure longitudinal ridges.

Rarely collected small trees of evergreen forest formations from (0) 400 to 2,000 m elevation; flowering from February to May in Costa Rica. The species has only been collected along the Pacific watershed in Costa Rica from the Nicoya peninsula and easternmost Guanacaste province to the General Valley and along the Pacific slopes of the Talamanca mountains. The species ranges from central Costa Rica into Panama and probably into northern South America.

*Guapira costaricana* is recognized by the often unequal opposing leaves (occasionally in whorls of 4), the reddish puberulent terminal inflorescences with very small tubular female flowers and exerted fimbriate stigmas or slightly larger campanulate male flowers with exerted stamens, and the fruit becoming dark purple or black on a red inflorescence. These plants are restricted to central and southern Costa Rica along the Pacific slope and have not been collected in the same areas as our representatives of *Neea*, as if they were excluding each other from the same habitat. The reason for making such a remark is that *Neea* has a rather unusual distribution in Costa Rica and, in addition, our species of *Guapira* and *Neea* should probably be united in the same genus. With very dark fruit on bright red inflorescences, one would expect these plants to be collected more often; they appear to be restricted to tropical moist premontane wet forest formations and to flower only in the dry season.

#### MIRABILIS Linnaeus

Herbs or small shrubs, perennial but often capable of flowering after only a few months growth (annual), sometimes woody near the base, usually much branched, the nodes often thickened, rootstocks often tuberous; stipules absent. Leaves opposite and simple, petiolate (in ours) or sessile, entire or undulate, pinnately veined. Inflorescences mostly small cymes or clusters of bracteate flowers in leaf axils or terminal, with 1 or several flowers subtended by leaflike bracts that are united near the base and form a 5-parted calyx-like involucre (the product of a reduced cyme); flowers bisexual and radially symmetrical, perianth united and forming a campanulate to funnelliform or salverform tube, the tube short or long, 5-lobed at the apex and induplicate-valvate in bud, the upper portion deciduous, stamens 3–5, equaling or exceeding the perianth tube, filaments slender and unequal, short-connate at the base, ovary ovoid to globose, style slender with 1 long papillate or capitate stigma. Fruit included within the persisting and slightly enlarged bracteate (but calyx-like) involucre, achene-like but said to be an anthocarp formed by adnation with the base of the perianth tube, cylindrical to obovoid, terete, with 5 longitudinal ridges or sulci, often rugose or tuberculate, glabrous or puberulent, constricted just above the base, mucilaginous when wet; embryo sharply curved.

A genus of perhaps 60 species, nearly all American. One species (*M. jalapa*) is now widely naturalized and planted for ornament. The opposite leaves that are often slightly viscid and triangular in outline, the bracteate calyx-like involucre subtending one or a few flowers, the showy corolla-like perianth tube usually bright reddish purple in color, and the unusual fruit distinguish this genus which can be mistaken for members of the "Tubiflorae" (Gentianaceae, Solanaceae, etc.). The genus *Oxybaphus* is no longer considered distinct from *Mirabilis*.



KEY TO THE SPECIES OF *Mirabilis*

- 1a Perianth tube 3.5 cm long; fruit 7–9 mm long; common plants of weedy and cultivated sites in evergreen and partly deciduous areas ..... *M. jalapa*
- 1b Perianth tube 0.5–1 cm long; fruit 3–4 mm long; plants restricted to the seasonally dry Pacific lowlands of central and northern Costa Rica. .... *M. violacea*

***Mirabilis jalapa* L., Sp. Pl. 177. 1753.**

Herbs or subshrubs to 1.3 m tall, annual or perennial, bisexual, much branched, leafy internodes 1–10 (15) cm long, 1–5 mm thick (dry), usually minutely (0.1–0.5 mm) puberulent with crooked brownish multicellular trichomes, the hairs often dense in longitudinal grooves and at the thickened nodes, occasionally glabrous. Leaves opposite and usually equal at a node, petioles 0.8–6 cm long, 0.5–1.5 mm broad (dry), with an adaxial sulcus or groove, usually sparsely puberulent; laminae 2–10 (14) cm long, 1–6 (8) cm broad, triangular to ovate-deltoid or ovate, tapering gradually to the acute or acuminate apex, rounded or abruptly truncate (subcordate) at the base, short-decurrent on the petiole, margins entire and often ciliate, the laminae drying membranaceous to thin-chartaceous, usually sparsely puberulent with scattered hairs 0.3–1 mm long between the veins and shorter dense hairs on the veins above, usually glabrous beneath, with 3–5 pairs of major secondary veins. Inflorescence cymose or glomerate in leaf axils or terminal, occasionally solitary and axillary, peduncles less than 5 mm long; flowers to 7 cm long, subtended by a sepaloid whorl of 3–5 partly united leaflike bracts 7–15 mm long, green and sparsely puberulent, the perianth with a long narrow tube and funnellform, to 6 cm long and 2.5–4 cm broad at the apex, usually deep fuchsia magenta, or purple-red, occasionally yellow, orange, pink, or white; stamens equaling or slightly exceeding the perianth. Fruit 7–9 mm long, ca. 5 mm thick, ellipsoid or ovoid, with 5 thin dark longitudinal ridges, dark brown and verrucose, with a slight constriction just above the base.

Cultivated plants in gardens and weeds of open early secondary vegetation, ranging from sea level to about 2,000 m in both evergreen and partly deciduous formations in Costa Rica; probably flowering throughout the year, but with collections made primarily from June to January. This species is now widespread throughout the tropics and subtropics both as an ornamental and a weed; its origin appears to have been in Mexico.

*Mirabilis jalapa* is recognized by its tubular, orange, white, or purplish flowers subtended by a calyx-like involucre of united bracts, opposite leaves with the larger laminae almost triangular in outline, and the usual association with cultivated or disturbed areas. Flowers of different colors are occasionally produced by the same plant, and a perianth with longitudinally striped colors is sometimes seen. The species is called *Maravilla* throughout Central America and "four-o'clock" in English-speaking countries.

***Mirabilis violacea* (L.) Heimerl, Beitr. Syst. Nyctag. 23. 1897. *Allionia violacea* L., Syst. ed. 10. 890. 1759. *Oxybaphus violaceus* Choisy, in DC., Prodr. 13, pt. 2:432. 1849.**

Herbs, erect, procumbent, or clambering to 1 m tall, annual or with a perennial rootstock, bisexual, leafy internodes (0.8) 1.5–9 cm long, 0.3–2 mm thick (dry), sparsely to densely puberulent with thin brownish multicellular or gland-tipped hairs, the trichomes often restricted to longitudinal grooves. Leaves opposite and equal at a node, petioles 0.5–3 (6) cm long, ca. 0.5 mm broad (dry), glandular puberulent, with 2 abaxial ridges forming a groove or sulcus above; laminae 1.5–5 (7) cm long, 1–3 (5) cm broad, ovate-triangular, to broadly ovate or narrowly triangular, tapering gradually to the acuminate (rarely obtuse) apex, rounded at the cordate to truncate base, margin entire, the laminae drying membranaceous to thin-chartaceous (sometimes slightly succulent in life), sparsely puberulent or minutely puberulent only on the veins above, usually glabrous beneath but with cystoliths conspicuous on the dried undersurface, with 2 or 3 pairs of major second-

ary veins. Inflorescences small terminal or axillary cymes (flowers sometimes solitary and axillary), usually congested but sometimes to 5 cm long and with peduncles or pedicels becoming 2 cm long, pedicels thin and densely covered with thin brownish or glandular hairs; flowers 10–15 mm long and subtended by a calyx-like involucre of broad green leaflike puberulent bracts 3–4 mm long and enlarging in fruit to 6 mm long, united near the base and with viscid hairs, perianth tube 5–10 mm long, 5-lobed, purplish or rarely white, stamens usually 3. Fruit narrowly obovoid or cylindrical, 3–4 mm long, 2–2.5 mm thick, dark brown, narrowed at the apex and constricted above the base, usually with paler-colored longitudinal ribs, puberulent.

Small plants of both open early secondary and weedy sites and in shaded woodland in the seasonally dry deciduous vegetation of the Pacific lowlands in Guanacaste and northern Puntarenas provinces; flowering collections have been made from mid-April to August in our area and from March to November in Nicaragua and Honduras where the plants are found as high as 900 m above sea level. The species ranges from southern Mexico along the Pacific side of Central America to the northern half of Costa Rica, Colombia, and Venezuela.

*Mirabilis violacea* is recognized by its small stature, opposite cordate to truncate leaves, bracteate involucre united at the base, pink-purplish perianth tube, usual presence of viscid hairs, and restriction (in our area) to the drier Pacific lowlands.

#### NEEA Ruiz & Pavon

Small shrubs to small- or medium-sized trees (rarely more than 8 m tall), unisexual, usually reddish brown puberulent in early stages, often becoming glabrescent. Leaves opposite or in whorls of 4 at flowering or branching nodes, occasionally subopposite or alternate on the same plant, leaves of the same node often differing in size, petiolate, laminae entire and pinnately veined, often slightly succulent in life. Inflorescences terminal (appearing axillary only with further growth of a subtending axillary twig), usually solitary at a node (rarely 2 or 3), paniculate or thyriform with a single slender peduncle and usually a single primary rachis with opposite to alternate primary branches, the flowers often in cymelike distal groups of 3, sessile or pedicellate and with 1–3 minute bracteoles at the base of the perianth tube, the inflorescence and its branches often bright red or purple. Male flowers with an ellipsoid to ovoid perianth tube with 5 small perianth lobes at the narrow apex of the tube, often semisucculent in life, stamens usually 8 (5–10), included within the perianth tube, filaments unequal in length and fused at the base, a pistillode present and often of normal size. Female flowers urceolate to tubular, the tube often constricted beneath the 5 small lobes, usually much smaller than the male flowers, staminodes present and with normal but nonfunctional anthers, pistil sessile or narrowed at the base, unilocular with 1 style and a single fimbriate stigma. Fruit a fleshy anthocarp formed by the succulent perianth tube tightly enclosing the ovary, bright yellow, pink, deep red or purple, free distal portion of the perianth tube usually deciduous, surface smooth but the longitudinal ribs often apparent when dry; seed with straight embryo and contorted cotyledon, little endosperm.

*Neea* ranges from southern Florida and central Mexico through Central America and the West Indies as far as Bolivia. These plants, with their shrubby or small tree habit, opposite leaves, and narrow tubular flowers resemble members of the Rubiaceae family, but that family has stipules, an inferior ovary, and a calyx and corolla. The terminal inflorescences of *Neea* often produce dichotomous branching as growth proceeds beyond the flowering node. The genus *Neea* may not be sufficiently distinct from *Guapira* to merit generic rank, in which case the species listed here would have to be transferred to *Guapira* (q.v.). I have seen no reference to the economic use of these plants, though it is said that the fruit have been used for coloring.

There seem to be no clearly defined species of *Neea* in Costa Rica. Even the most unusual plants can be related to more common forms by intermediate

collections. There may be more species than the two generalized concepts presented here, but variation is so great among the common forms that there is no way of clearly delimiting the rarer forms. This troublesome variability appears to affect all aspects of the plants: habit, leaves, pubescence, inflorescences, flowers, and fruit. Add to this the problem of relating specimens with male flowers to those with female flowers or fruit, and one can understand why identifying species (if such exist in *Neea*) is so difficult. I have illustrated and written a key to two "species groups"; these can then be further divided by using the brief subsidiary keys and the illustrations. However, the two "species groups," treated as two species in a wide sense in the descriptions, have the same flowering periodicity, the same altitudinal range, and similarly peculiar distribution patterns within Costa Rica. This seems to indicate that, however different some of these plants may look from each other, there may be no barriers to gene flow within the genus in southern Central America and, in effect, no real species.

#### KEY TO THE SPECIES GROUPS OF *Neea* IN COSTA RICA

- 1a Fruit of the lateral inflorescence branches sessile, subsessile or borne on relatively short thick pedicels shorter than the fruit; leaves becoming quite large (20–35 cm) and broadly obovate to broadly oblong or broadly elliptic (leaves shorter above 1,200 m elevation), glabrous or puberulent; small subshrubs, few-stemmed shrubs or small trees, 1–3 (8) m tall, often found in the deep shade of the forest understory  
*N. amplifolia* s.l.
- 1b Fruit of the lateral inflorescence branches borne on slender pedicels, the pedicels often becoming as long or longer than the fruit (terminal flowers and fruit often sessile); leaves rarely exceeding 18 cm in length, generally elliptic to elliptic-oblong (sometimes obovate in smaller leaved individuals), gradually tapering to both apex and base, usually glabrous; shrubs, small trees or rarely large (20 m) trees, often found in open secondary growth ..... *N. psychotrioides* s.l.

***Neea amplifolia*** Donnell Smith, Bot. Gaz. 61:386. 1916. *N. orosiana* Standl., J. Wash. Acad. Sci. 15:473. 1925. *N. urophylla* Standl., Publ. Field Columbian Mus., Bot. Ser. 4:203. 1929. *N. elegans* P. H. Allen, Rain Forests of Golfo Dulce 273 & 409. 1956. Figure 35.

Few-branched subshrubs or small trees, 0.4–2 m tall, unisexual, leafy internodes 0–10 cm long, 1–4 mm thick, soon becoming glabrous, smooth and pale colored in later stages. Leaves usually opposite, petioles 3–30 (65) mm long, with lateral ridges; laminae 8–26 (35) cm long (2) 5–12 (17) cm broad, obovate to broadly elliptic-oblong, less often broadly elliptic, oblong or ovate, usually abruptly narrowed to the apex, usually tapering gradually to the base, margin entire, surfaces smooth, glabrous or minutely puberulent beneath, with 6–13 pairs of major secondary veins. Inflorescences terminal, rarely more than 6 cm long in flower (to 10 cm in fruit, peduncle becoming 7 cm long in fruit). Male flowers 5–9 mm long; female flowers 2–4 mm long at anthesis, usually densely puberulent. Fruit rounded to oblong or ellipsoid, to 1 cm long when dry, usually borne on a pedicel shorter than the body of the fruit.

Small few-stemmed shrubs of forest shade in moist evergreen formations from sea level to 1,600 m elevation; flowering from April to November, but fruit have been collected from January to November. Distribution in Costa Rica is very similar to that of *N. psychotrioides*; throughout the Caribbean lowlands, along the northwestern volcanic chain to San Ramon and Zarcero, uncommon on the wet Caribbean slope near La Palma and Bajo La Hondura, Muñeco, Orosi, and Turrialba, and it has not been collected in the General Valley or on the Pacific slopes of southern Costa Rica. The species ranges from Nicaragua to Panama.



*Neea amplifolia* is recognized by its larger, obovate to very broadly elliptic-oblong leaves, short stature, small inflorescences, fruit borne on relatively short pedicels, and shaded forest habitat. There appears to be no way in which this taxon can be sharply distinguished from *N. psychotrioides*, and intermediate plants are found with some frequency. It may be that the plants placed here are no more than an ecotype found in deeply shaded sites. The two species, *N. amplifolia* and *N. psychotrioides*, share the same peculiar distribution pattern in Costa Rica, except that *N. amplifolia* is more common in the drainage area of the Rio Reventazon and appears to be absent from the Golfo Dulce area. Flowering periodicity is also nearly identical in the two entities. I believe that the extreme forms differ so greatly and with sufficient frequency that it may be useful to retain *N. amplifolia* at the level of species rank until we have a better idea of what is actually going on within and between these populations. *Neea acuminatissima* Standley with long (ca. 30 cm) leaves that taper very gradually to the acuminate apex may be a similar species of deeply shaded sites in the Caribbean lowlands of northern Central America.

*Neea pittieri* Standley (Contr. U.S. Natl. Herb. 13:383, 1911) appears to belong in this group and is the earliest name available. However, the type is rather atypical of the assemblage, and its restriction to higher elevations makes its placement provisional, hence, use of the name *amplifolia*.

#### POSSIBLE SEGREGATES OF *Neea amplifolia* (IN A WIDE SENSE)

- 1a Montane plants above 500 m elevation; leaves often very broad, occasionally obovate; shrubs 1–3 m tall. .... *N. pittieri* Standley
- 1b Lowland plants ..... 2a
- 2a Small plants (1–2 m tall) of the dark forest understory, leaves often obovate (to elliptic-oblong), often attacked by leaf miners. .... *N. amplifolia sensu stricto*
- 2b Larger plants usually becoming small trees; leaves rarely obovate; uncommon plants ..... 3a
- 3a Leaves very broadly oblong or elliptic-oblong, becoming glabrous in age  
*N. urophylla* Standley
- 3b Leaves elliptic to elliptic-oblong, remaining brownish puberulent in age  
*N. elegans* P. H. Allen

*Neea psychotrioides* Donnell Smith, Bot. Gaz. 16:199. 1891. *N. laetevirens* Standl., Publ. Field Columbian Mus., Bot. Ser. 4:204. 1929. *N. belizensis* Lundell, Contr. Univ. Michigan Herb. 7:9. 1942. *N. pycnantha* Standl., Ann. Missouri Bot. Gard. 30:85. 1943. *N. xanthina* Standl., loc. cit. 30:86. 1943. *N. popenoei* P. H. Allen, Rain Forests of Golfo Dulce 274 & 410. 1956. Figure 34.

Shrubs, small trees or occasionally subshrubs, 1–5 (8) m tall, unisexual, leafy internodes 0–6 (10) cm long, 1–4 mm thick, minute reddish brown tomentulose in early stages but quickly becoming glabrescent, smooth and terete, the older stems often pale grayish in color in contrast to the newer stems which often dry very dark. Leaves usually opposite, often in a whorl of 4 at branching or flowering nodes, occasionally alternate or subopposite on the same branch, opposing leaves of a node often slightly unequal, petioles 4–30 mm long, 0.4–1.6 mm thick, with 2 lateral ridges continuous with the lamina margins; laminae (2) 3–15 (23) cm long, 1.8–8 cm broad, generally elliptic to elliptic-oblong (obovate to ovate usually only in small-leaved plants of higher altitudes or seasonally very dry areas), tapering gradually or abruptly to an acute or short acuminate apex, tapering gradually or abruptly to an acute to obtuse base, often somewhat unequal at the base, margin entire, surface smooth and glabrous in age (occasionally remaining brownish puberulent beneath), with 5–11 pairs of major secondary veins, the midvein often pinkish or reddish in life. Inflorescences (3) 8–35 cm long, terminal (apparently axillary by continued growth of



a subtending stem), usually pendulous or becoming so in fruit, often a panicle with a long primary peduncle and openly dichotomous cymelike distal branches, the primary peduncle to 20 cm long and often exceeding the length of the flowering portion of the inflorescence, branches of the inflorescence usually minutely (0.1 mm) reddish brown puberulent, floral bracts 0.5–1 mm long, pedicels 0–5 mm long, often equaling or exceeding the flowers in length. Flowers deep red in bud but becoming yellowish white or greenish white, male flowers with a floral tube 4–7 (9) mm long, female flowers with a floral tube 2–3 mm long at anthesis. Fruit becoming 6–10 mm long (dry), ellipsoid to subglobose, ribbed when dry, pink to deep red.

Shrubs and small trees often found in secondary growth and openings in the forest interior; ranging from sea level to about 1,500 m elevation. The species appears to flower for much of the year, but we have very few flowering collections from November to January in Costa Rica. The species ranges from southern Mexico to Panama and probably extends into South America under a variety of other names. The geographic distribution of this species in Costa Rica is unusual. It is not uncommon in the northwestern highlands, as far east as San Ramon and Zarcero, but it has not been collected from the central volcanoes nor from the Talamanca range. Likewise, though common in the Caribbean lowlands, it is not known from the General Valley and appears to be quite uncommon in the evergreen forests along the Pacific in southern Costa Rica.

#### POSSIBLE SEGREGATES OF *Neea psychotrioides* (IN A WIDE SENSE)

- 1a Leaves usually less than 13 cm long; infructescences usually less than 10 cm long; Pacific slope of Central America southward to Guanacaste and the Sierra de Tilaran to the western edge of the Meseta Central, occasional in the Caribbean lowlands in open sites. .... *N. psychotrioides sensu stricto*
- 1b Leaves or the fruiting inflorescences larger than above; not known from northwestern Costa Rica or the Pacific slope of northern Central America ..... 2a
- 2a Peduncles and pedicels long and thin, pendulous from early stages, pedicels often greatly exceeding the fruit in length, fruit less than 10 mm long; leaves often quite narrow, rarely collected. .... *N. delicatula* auct. in herb.
- 2b Peduncles and pedicels not so thin, becoming pendulous in later stages(?) ..... 3a
- 3a Trees to 20 m tall, leaves often abruptly acuminate; male flowers to 7 × 4 mm on long inflorescences, fruit(?) to 2 cm long; rare. .... *N. popenoei* P. H. Allen
- 3b Shrubs or small trees, leaves usually tapering gradually or abruptly to the apex; male flowers smaller; fruit not so long; very common and intergrading with *N. amplifolia* ..... *N. laetevirens* Standley

#### PISONIA Linnaeus

Shrubs, small trees, or lianas, unisexual, glabrous or puberulent, axillary short straight or curved spines usually present, younger leaves often developing from the sides of the spines. Leaves opposite, subopposite, or occasionally in alternate nearby pairs, laminae decurrent on the petiole, simple and entire, venation pinnate. Inflorescences solitary or fasciculate, axillary or terminal on highly modified axillary short shoots, the flowers often borne in cymes but the cymes clustered in umbelliform, capitate, corymbiform, or other arrangements. Flowers small and radially symmetrical, greenish, unisexual, subtended by bracteolate pedicels; male flowers with a campanulate perianth tube, the tube with 5 obscure distal lobes or teeth, stamens 6–8 (10), exerted at anthesis, filaments slender, united near the base to form a small tube and adnate to the base of the pistillode; female flowers with a narrow perianth tube, staminodes often in the form of a dentate disk adnate to the narrowed base (stipe) of the pistil, ovary 1-locular and with 1 ovule, style narrow and with a fimbriate stigma. Fruit an anthocarp formed by the union of perianth tube and pistil, narrowly elongate, terete or 5-angled in cross section, with longitudinal rows of stalked glands in 1 or several ranks, the fruit at maturity usually borne on greatly elongated peduncle and pedicels.

A pantropical genus with species estimated to number between 15 and 50. The slender coriaceous fruit borne on elongated pedicels and with longitudinal rows of stalked glands are quite distinctive. These fruits are said to adhere to the feathers of birds with their viscid glands.

*Pisonia fasciculata*, described by Standley (Contr. U.S. Natl. Herb. 13:388, 1911), bears fascicles of little subcapitate inflorescences borne on short shoots and straight spines. The type was collected by C. Wright on the Pacific side of Nicaragua between 1853 and 1856. This species appears to be a rare endemic of Central America's seasonally very dry Pacific lowlands, and it might possibly occur in northwestern Guanacaste.

- 1a Spines usually curved, stems and leaves glabrous or puberulent, laminae often obovate; fruit 15–20 mm long; shrubs, trees, or lianas in both deciduous and evergreen formations, 0–1,000 (rarely to 1,800) m elevation ..... *P. aculeata*
- 1b Spines straight, stems and leaves glabrous, laminae usually narrowly elliptic; fruit 8–10 mm long; shrubs or small trees of evergreen montane forests, 1,000–2,200 m  
*P. silvatica*

*Pisonia aculeata* L., Sp. Pl. 1026. 1753. *P. aculeata* var. *macranthocarpa* Donn. Smith, Bot. Gaz. 16:198. 1891. *P. macranthocarpa* Donn. Smith, Bot. Gaz. 20:293. 1895. *P. grandifolia* Standl., Contr. U.S. Natl. Herb. 13:391. 1911, not *P. grandifolia* Warb., 1891. Figure 33.

Shrubs or small trees to 10 m tall, often with clambering branches, becoming large lianas in evergreen formations, unisexual, leafy internodes 0.1–6 (12) cm long, 0.7–6 mm thick, glabrous and reddish brown to densely puberulent or villous and yellowish brown or grayish, becoming lenticellate, the nodes slightly thickened and often bearing 1 thick recurved (less often straight) spine from each axil, newer leaves often borne from the side of the spine. Leaves opposite, subopposite, or occasionally alternate (on the same stem), the leaves often borne on short shoots in the axils of fallen leaves, petioles 2–40 mm long, often very variable on the same stem, with 2 adaxial ridges continuous with the lamina margins; laminae 2–15 cm long, 1.5–6 (9) cm broad, elliptic to obovate or obovate-orbicular, usually abruptly narrowed to an obtuse, acute or short-acuminate apex, gradually narrowed to the acute (less often obtuse) base and decurrent on the petiole, margins entire, the laminae drying thin- to stiff-chartaceous, smooth, glabrous to densely puberulent on both surfaces or often puberulent only along the midvein beneath, with 5–8 pairs of major secondary veins. Inflorescences solitary and axillary, 2–6 cm long, made up of little cymes in complex umbel-like or panicle-like arrangements, unisexual, very minutely puberulent to hirsutulous with trichomes 0.05–0.5 mm long, often viscid, primary peduncles 1–4 cm long, pedicels subtended by small (1 mm) deciduous bracts, both peduncles and pedicels greatly elongating in fruit; male flowers with a campanulate perianth tube 2–4 mm long and ca. 3 mm broad, stamens 6 and exerted 2–3 mm beyond the perianth, anthers ca. 0.5 mm long; female flowers with a tubular or narrowly urceolate perianth tube 2–3 mm long. Fruit borne on open few-branched expanded infructescences with pedicels 1–3 cm long, the anthocarp 1.5–2 cm long (in ours), 5–8 mm thick, ellipsoid to narrowly obovoid-clavate, 5-angled (in cross section), with 5 longitudinal ridges, each ridge or angle with 1–3 ranks of stalked viscid glands, surfaces between the ridges densely and very minutely (0.05 mm) pale grayish or yellowish velutinous.

Shrubs, small trees, or rarely vines in seasonally very dry deciduous formations or becoming large woody lianas in moist or wet evergreen formations, to about 1,000 (very rarely 1,800) m elevation in our area; flowering and fruiting from July to March, but with most of our collections made between November and February. The species ranges from the southern tip of Florida and Mexico, through Central America and the West Indies, to Ecuador and northern Argentina; the species is also found in central Africa, southern Asia, and the Philippines.

*Pisonia aculeata* is recognized by the opposite or subopposite leaves with variable petioles and decurrent lamina bases, the short thick usually curved spines, the unisexual flowers with small perianth tubes in dense little inflorescences, and the very unusual fruit on open few-branched infructescences. The species appears to present a very unusual correlation between life-form and habitat. In wet evergreen forests, the plants are described as woody lianas reaching the tops of tall trees, while in deciduous vegetation, the plants are nearly always shrubs or small trees. Also, the wet forest material is often densely puberulent and has larger broader leaves (as in *Skutch 4848* from the General Valley). We have very little material representing these wet forest lianas, and it may be that they differ in other ways and are worthy of taxonomic recognition as a subspecies or variety. This species is known as *Uña de Tigre* in Central America.

*Pisonia sylvatica* Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18:425. 1937.

Slender shrubs or small treelets, 1.5–4 m tall, unisexual, often much branched, leafy internodes 1–6 cm long, ca. 1–2 (4) mm thick, glabrous, pale in color and relatively smooth with very few lenticels developing, nodes slightly thickened; spines axillary, 0.5–1.5 cm long, ca. 1.5 mm thick at the base, straight, smooth and sharp-tipped. Leaves opposite, subopposite or in alternate nearby pairs, petioles 3–10 mm long, ca. 1.3 mm thick, sulcate above with 2 adaxial ridges continuous with the lamina margins; laminae 4–10 (13) cm long, 2–4 (5) cm broad, elliptic, narrowly ovate-elliptic, or narrowly oblong-elliptic, tapering gradually to the acuminate or less often acute apex, tip usually blunt, tapering to the acute base, margin entire and decurrent on the petiole, the laminae drying stiffly chartaceous, smooth and glabrous on both surfaces, the midvein raised above, the 4–7 pairs of major secondary veins obscure on both surfaces. Inflorescences axillary and solitary, a cluster of small cymes on a long peduncle resulting in a capitate appearance in early stages, peduncles 1–4 cm long, glabrous but the pedicels papillate-puberulent; male flowers ca. 4 mm long and borne on pedicels to 3 mm long, the perianth tube campanulate with the usually 10 stamens extended 2–4 mm beyond the tube, anthers ca. 0.5 mm long; female flowers 2–3 mm long (dry), perianth tube minutely papillate puberulent, style and fimbriate stigma exerted. Fruit borne on pedicels elongating to 3 cm and becoming reddish, body of the fruit (anthocarp) 8–10 mm long, 3–4 mm thick (dry), narrowly ellipsoid to ellipsoid-cylindrical, style and stigma persisting and exerted, with 10 longitudinal rows of single-ranked stalked gland-tipped projections ca. 0.5 mm long.

Shrubs and small trees of evergreen premontane and lower montane moist forest formations between 1,000 and 2,200 m elevation; flowering and fruiting collections have been made from October to December and February and March. This species is known only from the areas near Monteverde in the Sierra de Tilaran and from near San Ramon and Zarcero on the western edge of the Meseta Central in Costa Rica.

*Pisonia silvatica* is recognized by the glabrous parts (except for the flowering parts of inflorescences), opposite to subopposite leaves with straight axillary spines, closely clustered flowers on a distinctive peduncle, and the fruit borne on greatly elongated pedicels and with 10 longitudinal rows of stalked glands. It is interesting that this endemic has never been found in areas east of Zarcero where collecting has been extensive; it may occur in the Sierra de Guanacaste which has been little collected.

#### SALPIANTHUS Humboldt and Bonpland

Herbs or small shrubs, usually much branched, bisexual, usually glandular puberulent, at least near the inflorescences; stipules absent. Leaves alternate and simple, laminae usually decurrent on the petiole, entire. Inflorescences small racemes, cymes or congested clusters, often in distal paniculate arrangements, terminal or axillary, bracts subtending



the flowers very small and inconspicuous; flowers bisexual and radially symmetrical, sessile or pedicellate, perianth tube cylindrical to urceolate, subcoriaceous, with 4 or 5 short lobes, covered with gland-tipped hairs (uncinate hairs present in ours), with 4 or 5 longitudinal ribs, not enlarging in fruit, stamens 3 and borne from 1 side of the perianth tube, filaments often unequal, anthers rounded, ovary sessile and with a slender style, stigma simple and acute, ovule solitary and basal. Fruit an achene-like utricle, the persisting glandular-pubescent perianth tube tightly enclosing fruit and seed; seeds very smooth and lustrous.

A genus of a few, principally Mexican, species. *Salpianthus* is closely related to *Mirabilis* among our representatives of the family, but lacks the corolla-like tube and subtending bracteate involucre. The broad basal triangular leaves, gland-tipped hairs on distal parts, stiff calyx tube (perianth tube) with hooked hairs, 3 stamens with thin filaments and rounded anthers exceeding the tube, and shiny black seed tightly enclosed in the persisting perianth tube help to distinguish our species of this genus.

***Salpianthus purpurascens* (Cav.) Hook. & Arn., Bot. Beechey Voy. 308. 1837.**  
*Boldoa purpurascens* Cav. ex Lagasca, Gen. & Sp. Nov. 10. 1816. *B. ovatifolia* Lag., loc. cit. Figure 32.

Herbs or subshrubs to 1.5 (2) m tall, much branched, leafy internodes 1–10 cm long 1–7 mm thick, glabrous or very minutely puberulent, angulate, the distal inflorescence bearing stems densely viscid puberulent. Leaves alternate, very variable in size on the same plant with smaller leaves on the distal flowering stems, petioles 0.3–10 cm long, with lateral ridges becoming winglike distally and continuous with the lamina margins; laminae 2–20 cm long, 1.5–18 cm broad, ovate to ovate-triangular or rhombic-ovate, tapering gradually to the bluntly acute or obtuse apex, rounded and truncate to subtruncate above the cuneate and long decurrent base, margins entire, the laminae drying thin-chartaceous, very minutely (0.1–0.2 mm) puberulent above, very minutely puberulent or glabrous beneath, short linear cystolith-like projections on the dried surface beneath, with 3–6 pairs of major secondary veins, the basal secondaries often very prominent and the venation subpalmate. Inflorescences small (1–5 cm) terminal and axillary panicles of short racemes or glomerules, peduncles and pedicels covered with small (0.2–0.3 mm) gland-tipped hairs; flowers sessile or subsessile, perianth tube 3–4 mm long, ca. 1.5 mm in diameter, narrowly urceolate to tubular, perianth lobes obtuse, perianth covered with both gland-tipped and sharply hooked (uncinate) trichomes. Fruit tightly enclosed within the persisting (but not enlarged) perianth ca. 3 mm long; seed ca. 1.5 mm long, suborbicular in outline, thick lenticular, lustrous black.

Plants of open fields and partly shaded woodlands from sea level to about 300 m elevation in Costa Rica; flowering from June to January in southern Central America. The species ranges from Mexico along the Pacific side of Central America to Guanacaste Province in Costa Rica, and it also occurs in Cuba and Venezuela.

*Salpianthus purpurascens* is recognized by its very broad ovate triangular leaves usually found at the base of the plant, the small flower clusters on distal stems with small leaves, the short narrow perianth tube with both gland-tipped and sharply hooked hairs on its surface, and the shiny black seed tightly enclosed within the persisting perianth tube. This species was earlier placed in the genus *Boldoa*.

## PHYTOLACCACEAE

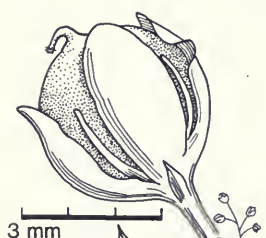
REFERENCES: Katherine Raeder, Phytolaccaceae in Flora of Panama. Ann. Missouri Bot. Gard. 48:408–421. 1961. Joan W. Nowicke, Palynotaxonomic study of the Phytolaccaceae. loc. cit. 55:294–364. 1969.



TRICHOSTIGMA  
polyandrum



T. octandrum



RIVINA humilis



MICROTEA debilis

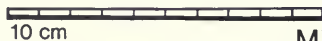


FIG. 36. Phytolaccaceae: Costa Rican representative of *Microtea*, *Rivina*, and *Trichostigma*.

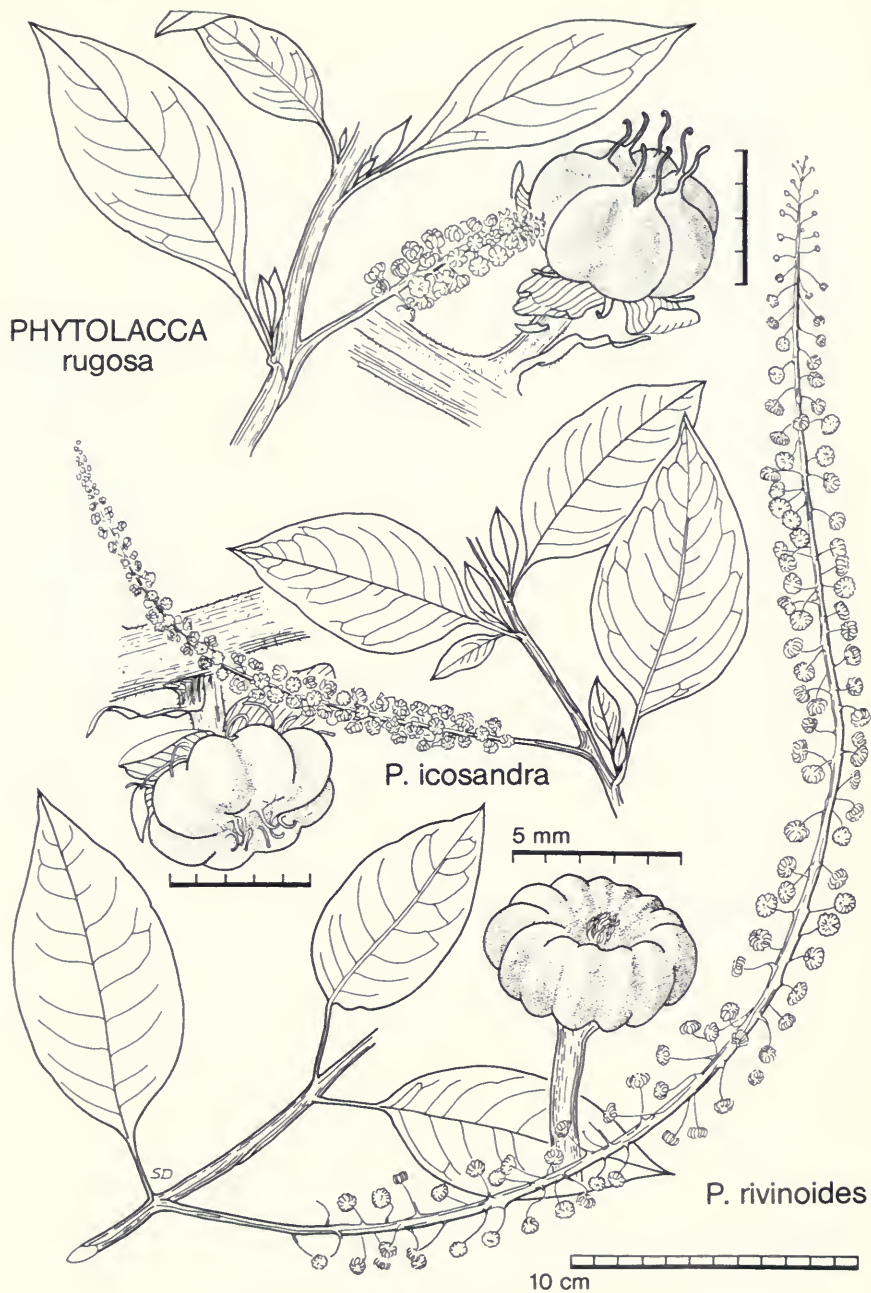


FIG. 37. Phytolaccaceae: three species of *Phytolacca*.

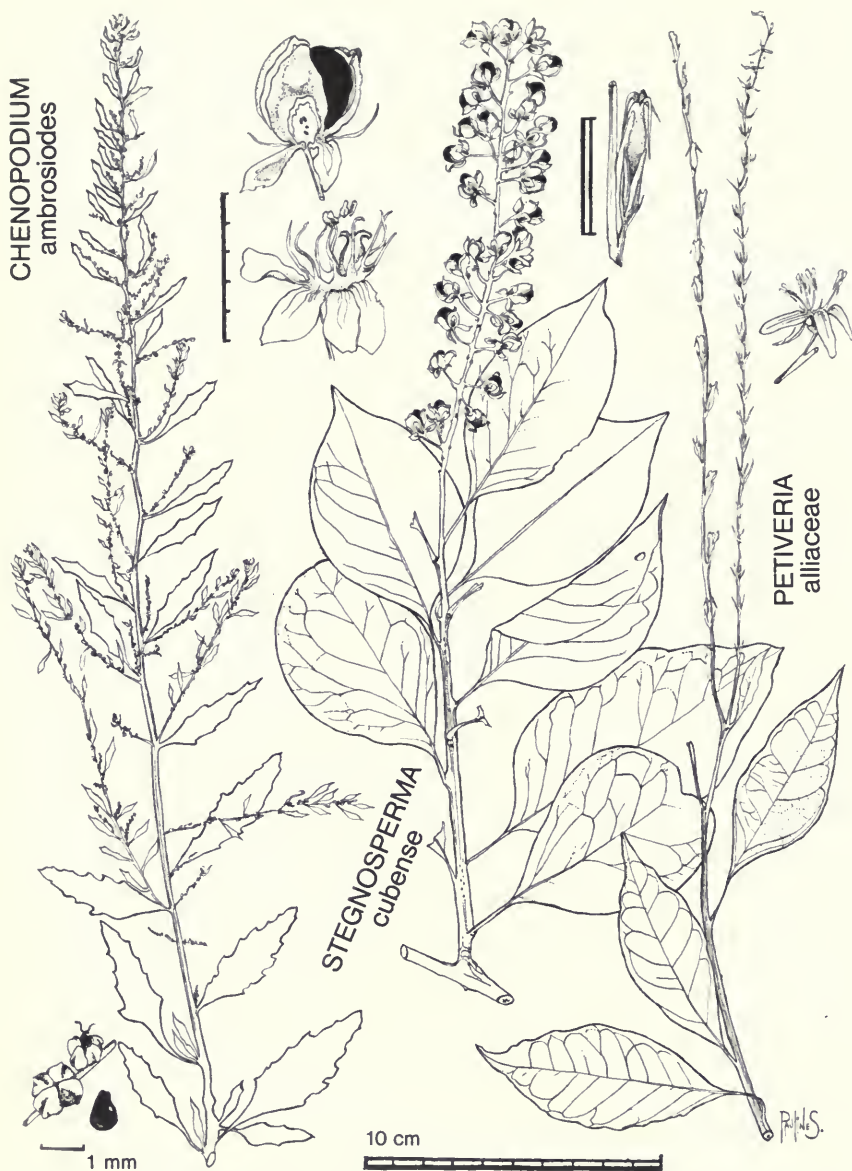


FIG. 38. Phytolaccaceae and Chenopodiaceae: a species of *Chenopodium* and species of *Petiveria* and *Stegnosperra* of the Phytolaccaceae.

Herbs or succulent subshrubs, erect or clambering, rarely larger woody shrubs or trees, bisexual (in ours) or less often unisexual, glabrous or sparsely and minutely puberulent; stipules absent or small and usually inconspicuous. Leaves alternate, simple and entire, pinnately veined, often with short linear crystals within. Inflorescences terminal, axillary or leaf-opposed usually solitary, racemose, spicate or compound paniculate with spicate or racemose branches, bracts and minute bracteoles present or absent; flowers small and bisexual in ours (unisexual by abortion), radially symmetrical or rarely somewhat bilaterally symmetrical, perianth usually of 1 whorl of 4 or 5 (rarely more) perianth parts (sepals or tepals), free or united near the base, imbricate in bud, usually persisting in fruit, greenish white to pink or purple, stamens often as many as the perianth parts and alternate with them or 3 to many and variously arranged, filaments free or united only at the base, often borne on a hypogynous disk, slender, anthers 2-thealous, dorsifixed or basifixed, dehiscent laterally; pistil simple or compound, 1-carpellate (unilocular) or of 2 to many carpels free or variously united, each locule with a single basal ovule, stigmas linear to capitate, sessile or borne on a short style. Fruit various, made up of 1 or more free or united carpels, fleshy or dry (rarely winged), subtended by the persisting perianth; seed subglobose to lenticular or reniform, erect, embryo annular or curved, endosperm present.

A family of about 17 genera and 70 to 80 species, with the majority of genera and species confined to the South American tropics. The flowers are characterized by a single perianth whorl that persists in fruit, and stamens alternating with the perianth parts when of the same number. However, the number of stamens and carpels varies greatly, occasionally on the same plant. The locules of the ovary always have a single basal ovule that produces a curved or annular embryo. The vegetative parts are often semisucculent and glabrous or only very sparsely puberulent.

The genus *Hillieria* is not known to occur in Central America or Panama. *Hillieria subcordata* Standl. & L. O. Wms., described in *Ceiba* 3:199 (1953), was based on a collection from Turrialba (*J. Leon* 3488), and this is undoubtedly a specimen of *Scutellaria* of the Labiatae family with immature flowers. Species of the genus *Hillieria* differ from all our representatives of the family in having a bilaterally symmetrical perianth with 3 united perianth parts and 1 free perianth part. The plants are similar to *Rivina*, but with more densely flowered racemes and a dry somewhat flattened fruit.

*Agdestis clematoides* Mocino & Sesse ex DC. from Mexico and northern Central America is similar to our species of *Trichostigma*, but the pistil is partly inferior and has three or four stigmas that become recurved; the leaves are usually subcordate and the inflorescences become white. This species is sometimes planted as an ornamental climber, but it has not been recorded from southern Central America. Its common names are *Bejuco de ajo* and *Vomita* because of the plant's unpleasant odor when crushed.

#### KEY TO THE GENERA OF PHYTOLACCACEAE

- 1a Flowers subsessile on long open spikes; fruit a narrow achene with 4 sharply retrorse spines at the top, partly enclosed by the dry persisting appressed perianth; usually found below 500 m elevation ..... *Petiveria*
- 1b Flowers borne on easily seen pedicels in open racemes or panicles; fruit without spines, usually globose, persisting perianth not ascending appressed ..... 2a
- 2a Perianth of 5 or 10 parts; ovary with 2–15 stigmas ..... 3a
- 2b Perianth of 4 parts; ovary with a single stigma ..... 5a
- 3a Fruit a capsule splitting open with valves, usually with 1 seed; stamens 10; woody plants of the very dry deciduous lowlands of northern Guanacaste ..... *Stegnosperma*
- 3b Fruit a berry or drupe, not splitting by valves; herbs and subshrubs not known to occur in drier northern Guanacaste ..... 4a



- 4a Succulent subshrubs 0.3–4 m tall; ovary with 5–15 locules and 5–15 stigmas, fruit a fleshy berry with 5–15 seeds; stamens 6–30; common plants from 0–3,300 m elevation ..... *Phytolacca*
- 4b Small semisucculent herbs to 0.8 m tall; ovary with 1 locule and 2 stigmas, fruit small and globose with spiny ridges forming a reticulum on the surface; stamens usually 5 (3–9); uncommon plants, below 500 m elevation ..... *Microtea*
- 5a Herbs or subshrubs with erect stems; stamens 4; fruit becoming bright red. . . *Rivina*
- 5b Woody climbers or shrubs with clambering stems; stamens 8 or more; fruit usually becoming black ..... *Trichostigma*

### MICROTEA Swartz

Small annual herbs, erect or decumbent, stems usually somewhat succulent and glabrous; stipules absent or represented by minute tubercles. Leaves alternate and usually small, petiolate or subsessile, laminae simple and entire, glabrous. Inflorescences terminal and axillary, 1 to several at a node, racemose, spicate or paniculate, with floral bracts and with or without bracteoles; flowers very small, bisexual, sepals 5 (4), free above a thickened receptacle, persisting in fruit, stamens 5 (3–9), usually alternating with the perianth parts, free or united near the base, anthers dorsifixed, thecae globose and dehiscent laterally, ovary with 1 locule and 1 ovule, style short, stigmas 2 or 3. Fruit fleshy or hard, smooth to tuberculate or echinate, the pericarp adhering to the seed; seed erect, embryo curved, endosperm fleshy.

A neotropical genus of nine species, with only one species reaching continental North America. The plants resemble some small Caryophyllaceae and slender stemmed Chenopodiaceae.

***Microtea debilis* Swartz, Prodr. Veg. Ind. Occ. 53. 1788. Figure 36.**

Annual herbs, 15–80 cm tall, usually much branched with prostrate or ascending stems, leafy internodes 0.5–3 (5) cm long, 0.5–2 mm thick and pale greenish gray when dry, longitudinally ribbed and glabrous, somewhat succulent in life. Leaves alternate and often distichous, slightly succulent, petioles 2–20 mm long, poorly differentiated from the blade with lateral margins continuous with the lamina margins; laminae 0.6–4 (8) cm long, 0.5–2 (3.5) cm broad, elliptic to obovate or ovate, bluntly obtuse to acute at the apex, attenuate at the base, margin entire, the laminae drying thin chartaceous to membranaceous, smooth and glabrous on both surfaces, the 4–7 pairs of major secondary veins arising at angles of ca. 40°–60°. Inflorescences terminal or axillary, often 2 (1) at a node, 1.5–6 cm long, open racemes or occasionally paniculate with 2 racemose axes, rachis 0.1–0.4 mm thick (dry), glabrous, flowers on short (0.3–2 mm) thin pedicels, subtended by membranous linear bracts ca. 1 mm long; flowers ca. 1 mm long, tepals 5, narrow, borne on the edge of a short receptacle, white, 0.5–0.7 mm long, stamens ca. 0.4 mm long, ovary ca. 0.5 mm long, glabrous. Fruit globose, greenish, ca. 1.5 mm long, with a reticulum on the surface formed by interconnected ridges of tubercles, subtended by the persisting perianth parts; seed black.

Uncommon weedy little plants of the wet evergreen lowland forest formations between sea level and 100 (300) m elevation on both the Caribbean and Pacific coastal plains of Costa Rica; probably flowering throughout the year, but collections from our area have only been made from December to May and in August. The species ranges from Guatemala and the West Indies to Peru and Brazil.

*Microtea debilis* is recognized by its small habit, glabrous slightly succulent parts becoming very thin when dried, alternate leaves with winged petioles, minute flowers on open racemes, and unusual little fruit with reticulate surface. This species has only been collected a few times in Costa Rica: from the Caribbean lowlands and the Golfo Dulce region. The plants appear to prefer sandy soils and are often found along stream and river banks.

## PETIVERIA Linnaeus

Erect herbs or subshrubs, woody at the base, minutely puberulent or glabrescent, stems with longitudinal ridges, tissues often with the odor of garlic (*Allium sativum*); stipules paired and lateral. Leaves alternate in a spiral or distichous, petioles canaliculate adaxially, the laminae simple and entire, acute to acuminate. Inflorescences slender elongate spike-like racemes of distant flowers subtended by short bracts, terminal or axillary and solitary or several from a node, the flowers very short pedicellate or subsessile; flowers bisexual and radially symmetrical, small, perianth of 4 free parts, equal and acute, narrow, spreading at anthesis, persisting and erect in fruit, stiff and dry, stamens 4–9, alternate with the perianth parts or irregularly placed, shorter than the perianth, filaments filiform, anthers dorsifixed and linear, 2-cleft at apex and base, ovary unilocular with 4 or 6 reflexed spines near the apex, stigma solitary, sessile and penicillate, ovule erect. Fruit a long narrow cuneate achene, laterally compressed with 2 slightly flattened carinate sides, apically 2-lobed with 4 or 6 retrorse or recurved spines, pericarp adhering to the seed; seeds erect and linear.

A New World genus of one species with two varieties: one widely ranging throughout the warm areas of the hemisphere and the other in Brazil. The plants resemble certain *Amaranthaceae*. *Petiveria* is distinguished from the *Amaranthaceae* because it lacks stamens that are equal in number and opposite to the perianth parts and because the stamens are not basally united.

***Petiveria alliacea* L., Sp. Pl. 342. 1753. Figure 38.**

Herbs or small subshrubs, 0.5–1.5 (2) m tall, base and lower stems woody, leafy internodes 1–6 cm long, 1.5–4 cm thick, minutely (0.1–0.3 mm) puberulent with slender ascending pale-colored hairs, longitudinally ridged; stipules ca. 2 mm long and 0.4 mm broad, persisting, brownish. Leaves alternate in a spiral or distichous, petioles 4–18 mm long, ca. 1 mm thick, minutely puberulent, with an adaxial sulcus; laminae 5–16 (20) cm long, 2–6 cm broad, elliptic to elliptic-oblong, short acuminate at the apex (occasionally acute), acute at the base, the margins entire, the laminae drying thin to stiffly chartaceous, smooth above and below, sparsely and very minutely puberulent along the veins but often becoming glabrous, the 5–8 pairs of major secondary veins arising at angles of 40°–70°. Inflorescences 1–5 in terminal groups or axillary, slender spikes 10–40 cm long, the flowers 5–15 mm distant on the slender (0.5–1 mm) sparsely puberulent rachis, flowers subtended by scarious triangular bracts 1–2 mm long; flowers ca. 3–4 mm long, subsessile or on very short (less than 3 mm) pedicels, puberulent on the lower parts, perianth parts 4, white or greenish, stiff and scarious, 0.5–1 mm broad, stamens 8 (4, 6), free, to 3 mm long, ovary with 4 retrorse spines near the apex, stigmas 2. Fruit 6–8 mm long, somewhat flattened and oblanolate with a deep apical notch separating 2 lateral projections, each of which bears 2 (3) retrorse spines 1.5–3 mm long, greenish and longitudinally striate, minutely and sparsely puberulent, subtended by the persisting appressed bracts and perianth, the fruit and bracts and perianth appressed against the axis of the inflorescence, ascending.

Plants of weedy habitats in partly open as well as shaded sites in both seasonally dry and deciduous habitats and in wet evergreen formations from sea level to 300 (rarely to 1,500) m elevation in Costa Rica; probably flowering throughout the year, but collected with flowers and fruit in our area from August to February and in April and June. The species ranges from the southern United States through the West Indies and Central America to Argentina and Peru.

*Petiveria alliacea* is recognized by its small weedy habit with woody base, glabrescent alternate leaves, and long spikes with separate scarious flowers that resemble grass spikelets. The unusual fruit with four sharp recurved spines at the apex and vegetative parts that often smell like garlic (*Allium sativum*) further distinguish this species. Our material belongs to variety *alliacea* as defined by Nowicke. These plants are easily mistaken for members of the *Amaranthaceae*

family, while the inflorescences resemble those of some Acanthaceae and Gramineae. *Pseudelephantopus* of the Compositae also resembles this species.

### PHYTOLACCA Linnaeus

Herbs or subshrubs, rarely trees, bisexual in ours, stems erect or clambering, often somewhat succulent, glabrous or sparsely puberulent; stipules absent. Leaves alternate in a spiral, simple, sessile or petiolate, margin usually entire, usually glabrous, pinnately veined. Inflorescences at first terminal but soon becoming leaf-opposed or extra-axillary, spikes, racemes or raceme-like panicles, pedicels subtended by narrow bracts and often with 1 or 2 small bracteoles along the length of the pedicel; flowers small and radially symmetrical, bisexual (in ours) or unisexual, the perianth of 1 whorl of 5 usually free tepals, the tepals greenish or white to pink and purple, androecium of 5–30 stamens in 1 or 2 whorls, sometimes differing in number in flowers of the same inflorescence, filaments free or united at the base and borne on a disk, anthers dorsifixed; ovary usually broader than long, made up of a whorl of 5–16 partly or completely united carpels, the 5–16 locules with 1 erect ovule each. Fruit usually a fleshy and juicy berry, broader than long with a centrally depressed apex, 5- to 16-ribbed or parted; seed compressed, embryo curved.

A genus of worldwide distribution, but with most of the 30-odd species in the American tropics and a few species reaching the temperate zone. The broad gynoeceum with incompletely fused carpels, variable number of stamens, single perianth whorl, and solitary erect ovule are distinctive features. The semi-succulent stems and leaves and frequent presence of bright rose red to purplish pigments in vegetative parts and fruit are also characteristic. Hybridization has been suspected between many of the species. Plants of this genus resemble, superficially, *Sphenoclea zeylanica* Gaertn. (Campanulaceae or Sphenocleaceae) and some species of *Monnina* (Polygalaceae).

As can be seen in our illustration, *P. icosandra* is intermediate between *P. rivinoides* and *P. rugosa* in some respects. Jerold I. Davis, who has studied *Phytolacca* material from throughout Central America, believes that the earlier proposed species concepts can be placed in a linear arrangement, reflecting morphological transitions and hybridization, as follows: *P. rivinoides*, *P. icosandra sensu stricto*, *P. purpurascens*, *P. meziana*, *P. octandra*, *P. rugosa*, *P. costaricensis*. This sequence also reflects an altitudinal shift from lowland *P. rivinoides* to *P. costaricensis* above 3,000 m elevation, with *P. rivinoides* being most easily separated from among the group (Davis, personal communication, 1980). While hybridization and intergradation do exist, it is my impression that the keys and species descriptions provided here will effectively categorize a large majority of our Costa Rican collections and that hybrid populations or intermediate individuals are relatively rare in Costa Rica.

The fruit contain saponins and have been used as a substitute for soap in many areas. The common name *Jaboncillo*, widely used in Central America, reflects this usage. Other names used in our area are *Calalu* and *Tinta*, the latter referring to the pigments sometimes used as ink (mostly from the fruit). See the discussion of uses in the Flora of Guatemala (Fieldiana, Bot. 24, part 4:198, 1946).

- 1a Inflorescence axis glabrous, 15–80 cm long; ovary with more than 10 styles, fruit with more than 10 ribs, fruiting pedicels 5–18 mm long, styles closely connivent; 0–1,300 (1,800) m elevation . . . . . *P. rivinoides*
- 1b Inflorescence axis with small scurfy or scalelike hairs; ovary with usually 8 styles, fruit with usually 8 ribs or seeds, fruiting pedicels less than 6 mm long . . . . . 2a
- 2a Inflorescence axis 5–15 (20) cm long, pedicels 3–6 mm long; fruit with the styles 1–2 mm distant from the central apex; (1,500) 2,000–3,300 m elevation . . . . . *P. rugosa*
- 2b Inflorescence axis 10–36 cm long, pedicels 0.3–3 mm long; fruit with the styles close



together at the apex in the depressed center of the fruit; (500) 1,000–1,500 (1,800) m elevation ..... *P. icosandra*

***Phytolacca icosandra* L., Syst. Nat. ed. 10. 1040. 1759. Figure 37.**

Herbs or stout subshrubs to 1.5 (2) m tall, leafy internodes 3–40 mm long, (1) 2–8 mm thick, longitudinally ribbed when dry, glabrous. Leaves with petioles 5–30 mm long, ca. 1 mm thick (dry) and with lateral margins continuous with the lamina margins, decurrent on the stem; laminae (3.5) 5–15 (35) cm long, (1) 2–10 (18) cm broad, elliptic or occasionally ovate-elliptic, tapering to the sharply acute apex, the tip of thickened tissue drying yellowish and sharp-pointed, attenuate at the base and decurrent on the petiole, margin entire, the laminae drying thin chartaceous, smooth and glabrous on both surfaces, the 7–9 pairs of secondary veins arising at angles of ca. 45°–60°. Inflorescences usually becoming leaf-opposed (9) 12–25 (36) cm long, the raceme only 5–15 mm broad, elongating in fruit, peduncle 3–6 cm long, the rachis minutely scurfy-puberulent, drying yellowish but pink to purplish in life, pedicels 0.3–3 mm long, subtended by linear bracts 3–6 mm long and ca. 0.5 mm broad; flowers ca. 6 mm broad, perianth parts 2.5–3.5 mm long, white to pale purple, stamens (8) 16–18 (20), 3 mm long, styles usually 8 (6–10). Fruit becoming dark blue or black, ca. 8 mm broad and 4 mm long, the styles borne close together within the apical depression at the top of the fruit; seed lustrous black, lenticular, ca. 3 mm long and 2.5 mm broad.

Plants of recently disturbed secondary formations in and around the Meseta Central in Costa Rica; probably flowering throughout the year, but with no collections having been made in September. The Costa Rican collections come primarily from between 1,000 and 1,500 m elevation with only a few as low as 500 or as high as 1,800 m. The species ranges from Mexico and the West Indies to northern South America and Ecuador.

*Phytolacca icosandra* is recognized by the long narrow racemes with subsessile flowers, styles remaining close together as the fruit expands, and scurfy inflorescence axis. This species is quite similar to *P. rugosa*, but the two seem to be readily separable in our area. Recent collections made by Robert Wilbur and his associates from the area of the eastern Meseta Central and western Talamanca mountains indicate that there may be considerable intergradation between *P. icosandra* and *P. rugosa* between 1,500 and 2,500 m elevation.

***Phytolacca rivinoides* Kunth & Bouche, Ind. Sem. Hort. Berol. 15. 1848, and Ann. Sci. Nat. Bot. sér 3, 11:231. 1849. Figure 37.**

Herbs or weak stemmed subshrubs 1–2 (5) m tall, leafy internodes (1) 2–7 (11) cm long, 1.5–12 mm thick, glabrous and smooth, often reddish or pinkish in life, developing very small lenticels. Leaves with petioles (1) 2–7 cm long, slightly sulcate above and with lateral ridges continuous with the lamina margins and decurrent on the stem, often reddish in color; laminae 5–17 (21) cm long, 2–7 (9) cm broad, elliptic to ovate in outline, tapering gradually to the sharp-acuminate apex, acute to obtuse or somewhat rounded and subtruncate at the base, margin entire and decurrent on the petiole, the laminae drying thin-chartaceous, smooth and glabrous on both surfaces, often with small punctations above, the 6–11 pairs of major secondary veins arising at angles of about 60°. Inflorescence terminal and often becoming positioned just below an opposing leaf, 15–50 (80) cm long, the rachis essentially glabrous, peduncle 3–8 cm long, 1.2–2.4 mm thick, glabrous and smooth, pedicels 3–6 (13) mm long and subtended by thin lanceolate bracts ca. 3 mm long and with 1 or 2 minute bracteoles along the length of the pedicel, the rachis and pedicels smooth and glabrous, often pink to purplish; flowers ca. 5 mm broad (dry), perianth parts 2.5 mm long, white to rose or magenta, stamens 9–17; ovary usually green with 10–16 styles. Fruit borne on pedicels 5–18 mm long, ca. 0.5 mm thick (dry), fruit becoming 6–8 mm broad with 10–16 distinct longitudinal ribs, becoming blue or black when ripe, styles closely borne together in the depressed central apex; seeds lenticular, ca. 2 mm long, dull black, difficult to separate from the dry fruit.



Plants of open disturbed and early successional vegetation in wet and moist evergreen formations from sea level to 1,300 (1,800) m elevation in Costa Rica; flowering throughout the year. The species has not been collected below 500 m elevation in Guanacaste or northern Puntarenas. The species ranges from Mexico and the West Indies southward to Bolivia.

*Phytolacca rivinoides* is recognized by the smooth glabrous inflorescences that become unusually long, the fruit with 12 to 16 ribs, and a preference for moist habitats below 1,300 m elevation. Despite the distinct differences between this species and the other Costa Rican species, hybridization has been reported with *P. rugosa* at about 1,600 m near Cervantes.

***Phytolacca rugosa*** Br. & Bouche, Ind. Sem. Hort. Berol. 13. 1851, and Linnaea 25:296. 1852. *P. costaricensis* Suessenguth, Bot. Jahrb. Syst. 72:273. 1942. Figure 37.

Herbs or subshrubs 0.3–2 (4) m tall, the basal stems somewhat woody, leafy internodes 0.5–4 (10) cm long, 2–8 mm thick, glabrous or with scurfy hairs, longitudinally ridged when dry and the ridges continuous with the decurrent leaf bases. Leaves often closely approximate at the ends of stems in exposed and windy environments, petioles 0.2–3 (5) cm long, with thin lateral margins continuous with the lamina margins and decurrent on the stem; laminae (4.5) 6–12 (19) cm long, (1) 2–4 (6.5) cm broad, narrowly elliptic to elliptic-oblong, gradually tapering to the acute or sharply acuminate apex, acute at the base, margin entire and decurrent on the petiole, the laminae drying thin to stiffly chartaceous, smooth and glabrous or with scattered minute (0.1–0.2 mm) scurfy hairs on the veins beneath, the 6–8 pairs of secondary veins arising at angles of ca. 45°. Inflorescence terminal and becoming more or less leaf-opposed, 5–15 (20) cm long, at first with the flowers clustered in a compact conic raceme but soon elongating, peduncle 2–6 cm long and at first exceeding the flowering rachis in length, rachis and pedicels usually scurfy-rugose and drying yellowish but often bright pink or reddish purple in life, pedicels 3–6 mm long, subtended by linear bracts ca. 5 mm long, with 1 or 2 bracteoles along the length of the pedicel; flowers 4–5 mm broad (dry), perianth parts ca. 3 mm long, pink to reddish, stamens 6–12 in 1 cycle, 1.3–2 mm long, ovary with usually 8 styles. Fruit 6–10 mm broad and 2–4 mm high, green becoming dark purple, styles becoming 1–2 mm distant from the central depressed apex of the mature fruit; seeds lenticular, lustrous black, ca. 3.5 mm long and 2.5 mm broad.

Plants of recently disturbed and open early successional stages in evergreen highland forest formations between 1,500 and 3,300 m elevation; flowering and fruiting throughout the year. The species ranges from Mexico to Colombia.

*Phytolacca rugosa* is recognized by its relatively broad racemes with scurfy rachis and distinctly pedicellate flowers and the fruit with clearly separate styles borne some distance from the central apex. This is the only species of *Phytolacca* to be found commonly above 2,000 m elevation in Costa Rica. There may be hybridization between this species and *P. icosandra*.

An unusual collection by W. Hatheway (1358) from near the summit of Volcan Poas has the flowers borne on a superficially racemose inflorescence that is actually paniculate. The main axis bears short lateral flowering branches with several flowers, but this collection seems to differ in no other way from typical *P. rugosa*.

#### RIVINA Linnaeus

Perennial herbs or subshrubs, usually woody near the base, glabrous or minutely puberulent; stipules absent. Leaves alternate in a spiral, on slender petioles, simple and entire,

thin in texture, pinnately veined. Inflorescences erect solitary open racemes, terminal or becoming axillary, pedicels subtended by narrow little deciduous bracts, 1 or 2 minute bracteoles often present at the apex of the pedicel beneath the perianth, the inflorescence usually minutely puberulent; flowers bisexual and small, radially symmetrical, perianth of 4 subequal parts in 2 decussate whorls, slightly imbricate in bud, oblong spatulate and usually rounded at the apex, corolla-like and becoming white, persisting and enlarging only slightly in fruit, stamens 4, free, alternating with the perianth parts and inserted on the slightly elevated receptacle (hypogynous disk), slightly shorter than the perianth, anthers elongate and dorsifixed, extrorse-lateral, pistil simple, ovary with 1 locule and 1 basal ovule, style terminal or subterminal, often curved. Fruit a globose red drupe with pericarp adherent to the seed, subtended by the persisting perianth; seed lenticular, often with a covering of short hairs, embryo annular.

A genus of apparently only one somewhat variable species, probably of New World origin but now naturalized throughout the tropics. The genus is very closely related to *Trichostigma*, and some authors have treated the included plants as congeneric.

***Rivina humilis* L., Sp. Pl. 122. 1753. Figure 36.**

Perennial (occasionally annual?) herbs and shrubs 0.3–1 (rarely 2) m tall, usually woody at the base and sometimes with the lower stems woody, leafy internodes 1–8 cm long, 1–3 mm thick, glabrous or more often puberulent with thin whitish hairs 0.1–0.5 mm long, longitudinally ridged when dry and greenish; stipules absent. Leaves alternate in a spiral, petioles 0.4–4 (8) cm long, ca. 1 mm thick when dry, usually puberulent, with a slight adaxial groove above; laminae (2) 4–12 (17) cm long, (1) 2–6 (8) cm broad, ovate to elliptic-ovate or lanceolate, tapering gradually to the acuminate apex, rounded and truncate to rounded and obtuse at the base, margin entire, the laminae drying thin-chartaceous and usually greenish, smooth above and below, usually glabrous above (except on the midvein) and sparsely puberulent on the veins beneath, the thin pale-colored hairs ca. 0.2 mm long, linear crystals usually visible as minute (0.3 mm) prominent lines between the veinlets of dried leaves, the 5–7 pairs of major secondary veins arising from the midvein at angles of ca. 45°. Inflorescences terminal or axillary, racemes 4–12 (16) cm long (becoming longer after anthesis), rachis and pedicels usually with very short (0.2 mm) thin whitish hairs, bracts 1–2 mm long and deciduous, pedicels 2–4 mm long at anthesis and up to 8 mm long in fruit, slender and only ca. 0.2 mm thick when dry; flower buds ca. 2 mm long, perianth parts ca. 2 mm long, green becoming white or pinkish white, filaments 1–1.8 mm long, anthers ca. 0.7 mm long, ovary ca. 1 mm long with a style 0.5 mm long. Fruit becoming a bright red or orange globose fleshy drupe, 4–6 mm in diameter, subtended by the persistent and usually reflexed or spreading perianth parts (in late stages), the perianth parts to 4 mm long and 1–1.5 mm broad; the seed often with a reticulate surface formed by the adherent pericarp, seeds 2–2.5 mm broad, dark brown and with minute brownish hairs on the surface.

Plants of wet or seasonally dry evergreen formations or in moist situations (such as riparian understory) in deciduous areas between sea level and 1,200 (1,600) m elevation in Costa Rica; flowering throughout the year, but collected most often from December to January and June to September. The species ranges from the southern United States (Texas and Oklahoma to Florida) through Mexico and the West Indies to South America as far as Argentina; the species is widely naturalized in the Old World.

*Rivina humilis* is recognized by its short stature from a woody base, thin ovate leaves on slender petioles, open racemes, flowers with only four perianth parts and four alternating stamens, and simple pistil that forms a bright red drupe. The fruits are said to have been used as a source for red pigment. The plants resemble some small species of Solanaceae.

## STEGNOSPERMA Bentham

REFERENCES: H. G. Bedell, A taxonomic and morphological re-evaluation of Stegnospermaceae. Syst. Bot. 5:419–431, 1980. D. J. Rogers, *Stegnosperma*: A new species and a generic commentary. Ann. Missouri Bot. Gard. 36:475–477, 1949.

Shrubs or small trees, the branches often drooping, vining or clambering, bisexual, glabrous; stipules absent. Leaves alternate and simple, petiolate and entire, glabrous, often slightly succulent and drying stiff. Inflorescence racemose, terminal or axillary, solitary, the pedicels subtended by a bract and 2 bracteoles; flowers bisexual and radially symmetrical, borne on slender pedicels, perianth of 2 whorls, the 5 sepals free and imbricate, thin, persisting and enlarging slightly in fruit, petals or staminodia 5, free, shorter than the sepals, whitish, stamens 10, filaments slender but expanded near the base and connate to form a very short ring (perigynous annulus), anthers basifixed and sagittate; ovary superior and ovoid or ellipsoid, 3- to 5-locular but becoming unilocular with a central column, ovules basal, as many as the locules or style branches (stigmas). Fruit a globose or ovoid capsule, opening by 3–5 coriaceous valves, styles persisting; seeds 1–5, cochleate-ellipsoid, with a smooth dark reddish or black lustrous surface and a white or yellowish aril.

A genus of three species; two species are found only in Baja California and adjacent Mexico, while the third species ranges from Mexico to Costa Rica and the Greater Antilles. The capsular fruit, two perianth whorls, and woody habit distinguish this genus among our representatives of the family. The genus has only recently been found in Costa Rica. This genus has been elevated to family, but its position in the Caryophyllales remains the same, close to the putatively primitive Phytolaccaceae (see Bedell, 1980).

***Stegnosperma cubense*** A. Rich., in Sagra, Hist. Nat. Cuba 10:309; 12; tab. 44. 1845. *Trichilia scandens* A. Robinson ex Lunan, Hort. Jam. 2:319–320. 1814, an invalid polynomial (fide Rogers). *S. scandens* (Lunan) Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 23:6. 1943. Figure 38.

Small trees or shrubs with scandent or clambering stems, to 3 m tall or 4 m long, leafy internodes 2–20 mm long, 1–4 mm thick, smooth and glabrous, pale in color but soon becoming dark. Leaves alternate in a spiral, petioles 5–12 mm long, deeply sulcate above with 2 longitudinal adaxial ridges continuous with the laminae margins; laminae 2–8 (11) cm long, 1–5 (7) cm broad, obovate to orbicular or elliptic, obtuse to rounded at the apex, obtuse to acute at the base and decurrent on the petiole, margins entire, laminae drying stiffly chartaceous, smooth and glabrous, with 3–5 pairs of major secondary veins (often obscure). Inflorescences 3–13 cm long, the flowers closely crowded or separated by as much as 5 mm on the slender rachis, bract and bracteoles 1–1.5 mm long, pedicels 2–12 mm long; flowers 4–6 mm long (dry), sepals 3–4 mm long, broadly imbricate, petals included within the sepals, filaments 3–4 mm long, slender and united near the base, anthers 1.5 mm long, styles and stigmas usually 4 (3–5), ca. 1 mm long. Fruit an ovoid to subglobose capsule 6–7 mm long, subtended by the persisting perianth and with persisting styles, often with only 1 seed per fruit; seed ca. 5 × 3 mm, cochleate-ellipsoid in outline, lustrous black, the surface smooth or slightly irregular.

Small trees or clambering shrubs in seasonally very dry deciduous formations of the northwestern Pacific lowlands in Costa Rica. This species ranges from northern Mexico to Guatemala and along the Pacific lowlands to Costa Rica and from Cuba to Puerto Rico in the West Indies.

*Stegnospermum cubense* is distinguished by its small rounded leaves, lack of pubescence, terminal racemes, conspicuous pedicels, small petals hidden by the sepals, and capsular fruit with shiny black seed. This species and genus were not known to exist in Costa Rica until the recent intensive surveys of Santa Rosa National Park in Guanacaste Province. These little trees with drooping branches

or shrubs with clambering branches often form thickets behind sand dunes and on rocky outcrops in northern Central America. Our specimen (*Liesner 2284*) has much larger leaves than most Central American material, and the staminal cup appears to be less well developed. More collections from Guanacaste are needed to determine whether the Costa Rican populations merit separate specific or subspecific status.

### TRICHOSTIGMA A. Richard

Shrubs or woody climbers, usually glabrous; stipules minute and caducous or not apparent. Leaves alternate in a spiral, petiolate, the laminae simple and entire, pinnately veined, chartaceous when dry. Inflorescences terminal or axillary, solitary, elongate open racemes, the flowers clearly pedicellate, bracts subtending the pedicels present and caducous or absent, the pedicels often with small bracts and 2 minute bracteoles; flowers bisexual and radially symmetrical, perianth of 4 subequal parts in 2 whorls, broadly imbricate in bud persisting and usually reflexed in fruit, becoming reddish, stamens 8–25, free, borne on the elevated receptacle (hypogynous disk), filaments slender, anthers dorsofixed, longer than wide, pistil simple with sessile or subsessile penicillate stigma, ovary 1-locular and with 1 ovule. Fruit a globose fleshy drupe, pericarp attached to the seed; seed solitary with annular embryo and curved cotyledons, erect.

A New World genus of three species closely related to and perhaps congeneric with *Rivina* (q.v.). The plants are recognized by their climbing or trailing stems with glabrous leaves, open inflorescences that become reddish or purple in fruit, flowers with only four perianth parts and eight to 25 stamens, and simple pistil forming a fleshy black fruit. Like *Phytolacca* the open inflorescence and its pedicels often become wine red or purplish in color. While differing primarily in floral characters, the two species found in Costa Rica are apparently most common in the same restricted area: the Sierra de Tilaran and its Caribbean drainage area.

- 1a Flowers with ca. 20 stamens, the filaments less than 0.5 mm long and never persisting in fruit, perianth becoming 5–10 mm long in fruit; the racemes becoming 10–25 cm long. .... *T. polyandrum*
- 1b Flowers with usually 10 stamens, the filaments to 3 mm long and often persisting beneath the fruit, perianth not exceeding 5 mm in length; racemes up to 15 cm long ..... *T. octandrum*

**Trichostigma octandrum** (L.) H. Walter, in Engler, Pflanzenr. IV, 83:109. 1909. *Rivina octandra* L., Cent. Pl. 2:9. 1756. Figure 36.

Scandent shrubs or lianas, growing to a height of ca. 10 m, leafy internodes 5–50 mm long, 1–5.5 mm thick, glabrous, often with prominent lenticels, grayish when dry. Leaves alternate in a spiral, petioles 1–5 cm long, 0.5–1 mm thick, deeply sulcate above (adaxially); laminae 6–15 cm long, 2–7 cm broad, elliptic to narrowly elliptic-oblong or narrowly ovate, acute to short-acuminate at the apex, acute at the base with the margins shortly decurrent on the petiole, margins entire, laminae drying chartaceous, smooth and glabrous on both surfaces, the 6–9 (12) pairs of major secondary veins arising at angles of 45°–70°, often loop-connected near the margins but difficult to see. Inflorescences solitary and axillary racemes, 5–11 cm long, peduncle and rachis glabrous, ca. 0.5 mm thick and longitudinally striate when dry, peduncle (distance to the first flower) usually 2–3 cm long, pedicels 3–6 mm long and 1–6 mm distant on the rachis, with a linear bracteole ca. 2 mm long halfway up the pedicel; flowers ca. 4 mm long, perianth parts ca. 4 mm long, white, stamens usually 12 with anthers ca. 2 mm long borne on persisting filaments 2–3 mm long; pistil 1.5 mm long, the penicillate stigma ca. 0.5 mm long. Fruit becoming 8 mm long, globose, black, succulent, surface venation not readily visible when dry.



Plants of wet evergreen forest formations on both the Caribbean and Pacific sides of Costa Rica between 10 and 800 (1,000) m elevation; fruiting collections have been made from January through April. This is a wide-ranging species found from Mexico and southern Florida (U.S.A.) through Central America and the West Indies to Argentina.

*Trichostigma octandrum* is recognized by the climbing stems, glabrous parts, racemose inflorescences with slender rachis and pedicels, numerous stamens persisting as filaments with the fruit, and black succulent drupes. While relatively few collections of this species have been made in Costa Rica, it is interesting to note that many of these come from the same areas where collections of the congener, *T. polyandrum*, have been made: Tilaran and the areas bordering the San Carlos plain. However, this species has been collected in the Golfo Dulce area, and *T. polyandrum* has not. The relationship between these two species growing in the same areas and the differences in their flowers might make an interesting study.

***Trichostigma polyandrum* (Loes.) H. Walter**, in Engler, Pflanzenr. IV, 83:112. 1909. *Rivina polyandra* Loesner, Bot. Jahrb. Syst. 23:123. 1896. Figure 36.

Scandent or erect shrubs 1–3 (5) m tall, the stems usually clambering, leafy internodes, 0.5–16 cm long, 0.8–3 mm thick, glabrous or less often very minutely (0.1 mm) puberulent with straight erect hairs, becoming longitudinally ridged when dry. Leaves alternate in a spiral, closely spaced on lateral stems as well as widely spaced on long climbing stems, petioles (0.6) 1–3 cm long, 1–2.5 mm thick, broadly to narrowly canaliculate above; laminae 7–16 (18) cm long, 2–7 (9) cm broad, narrowly ovate to elliptic-ovate, acuminate at the apex, obtuse to acute or occasionally rounded at the base, margin entire, the laminae drying thin-chartaceous, smooth and glabrous above and below or with very minute erect hairs on the veins beneath, the 5–8 pairs of major secondary veins arising at angles of 60°–80°, arcuate ascending distally and often loop-connected near the margin. Inflorescences terminal or axillary, open racemes of distant flowers 7–15 cm long and becoming up to 25 cm long in fruit, peduncle and rachis glabrous or occasionally very minutely (0.1 mm) puberulent, 0.3–1 mm thick (dry) and reddish or purple after anthesis, pedicels (3) 6–12 (20) mm long with a small (1 mm) linear bracteole on the basal half, larger (2 mm) bracts subtending the pedicel sometimes present in early stages and caducous, 2 minute (0.5 mm) bracteoles sometimes present on the distal half of the pedicel; flower buds 2–4 mm long, green to pale greenish white, perianth becoming 6–10 mm long in fruit and rose to red or purple in color, stamens 20–25 with very short (0.5 mm) filaments and anthers ca. 1.5 mm long, quickly caducous after the flower opens, pistil 3 mm long and 1 mm thick. Fruit 5–8 mm long and equally broad, broadly ellipsoid or ovoid, becoming black, succulent but with the veins prominent on the outer surface when dry, subtended by the 4 persisting and brightly colored perianth parts.

Plants of evergreen wet forest formations of the Caribbean slope and lowlands, from sea level to 1,000 (rarely 1,500) m elevation; flowering and fruiting collections have been made from January to October in Costa Rica. This species is especially common in the wetter parts of the Sierra de Tilaran and the Caribbean lowlands of Alajuela Province; the species ranges from southern Nicaragua to western Panama.

*Trichostigma polyandrum* is recognized by its climbing stems, long fruiting inflorescences with distant and long-pedicellate fruit usually subtended by four red or purplish perianth parts. This species is more commonly collected than *T. octandrum* in our area, perhaps, because it has a longer flowering and fruiting season.

## AIZOACEAE

Herbs or subshrubs (rarely shrubs), annuals or perennials, prostrate or erect, stems and leaves often succulent, glabrous or puberulent; stipules small and thin or absent. Leaves alternate, opposite or whorled, simple and entire, equal or unequal at a node, sessile or petiolate, petioles often with a thin sheathing margin at the base; laminae often fleshy, sometimes reduced to scales. Inflorescences cymose or the flowers solitary, in the axils of leaves or terminal, flowers sessile or pedicellate, bisexual (rarely unisexual), small (in ours), radially symmetrical, perianth usually of 1 whorl of 5 (less often 3 or 4) free or united sepals (tepals), often with an extension or appendage on the back of the midvein distally, petals (actually staminodes) present and numerous in some cultivated and introduced genera but not in our native and naturalized species; stamens 3, 4, 5, 10 to many, alternate with the sepals when of the same number, filaments free or united into fascicles, rarely united to the perianth, anthers dehiscent longitudinally; pistil 1, ovary superior (in ours) or inferior, 1- to 5-locular (rarely 6- to 20-locular), placentation axile, basal, apical, or parietal but not free central, ovules 1 to many in each locule, styles as many as the locules, stigmas usually narrow, slender. Fruit a loculicidal or circumscissile capsule or indehiscent and nutlike or baccate; seeds cochleate to reniform, with mealy endosperm, rarely strophiolate, embryo usually curved.

The family, though a member of the very natural order Centrospermae (Caryophyllales), is not easily defined. Some of its genera appear to form links with the Caryophyllaceae, Portulacaceae, and Chenopodiaceae. The family is very diverse in southern Africa, with Australia a secondary center of diversity. Members of the family are rarely met with in the wild in Costa Rica. The unusual succulent forms from South Africa, with larger many-parted flowers, such as *Mesembryanthemum* (*sensu lato*) and the "flowering stones" are popular with gardeners and collectors of exotic plants. *Tetragonia expansa* Murr. (*Espinaca* or "New Zealand Spinach") is grown in Central America as a vegetable; the alternate slightly fleshy deltoid leaves are abruptly narrowed to the petiole and become as much as 12 cm long.

- 1a Leaves whorled or opposite, not very fleshy and not sheathing or clasping the stem; perianth parts free to the base; fruit a loculicidal capsule splitting longitudinally into 3–5 valves ..... 2a
- 1b Leaves opposite and fleshy, sheathing or clasping the stem at their base; perianth parts united to form a short tube, perianth lobes with small distal appendages; fruit opening by a transverse slit (circumscissile) with the distal lid or cap coming off, 1- to 5-locular ..... 3a
- 2a Plants usually puberulent with slender stellate hairs; leaves oblanceolate to obovate; flowers sessile or subsessile, perianth with slender distal appendages; seeds ca. 0.3 mm broad, strophiolate (with an aril-like development at the base) *Glinus*
- 2b Plants glabrous, leaves generally very narrow; flowers on slender pedicels; perianth without appendages; seeds ca. 0.5 mm broad, estrophiolate ..... *Mollugo*
- 3a Leaves linear to narrowly obovate, basal sheath sometimes united across the stem but without appendages, laminae equal or subequal at a node, young stems glabrous; ovary 3- to 5-locular, styles 3–5, seeds numerous, 0.5–1.5 mm broad ..... *Sesuvium*
- 3b Leaves obovate to rounded-spatulate, sheathing at the base and with an appendage on the united interpetiolar sheath, laminae often very unequal at a node, young stems often with a longitudinal ridge bearing crooked hairs; ovary 1- or 2-locular, styles 1 or 2; seeds less than 15, 1–2 mm broad. .... *Trianthema*

## GLINUS Linnaeus

Herbs, annual, procumbent or ascending, stems slightly succulent, often much branched, with simple or stellate hairs; stipules absent. Leaves opposite or whorled by

condensation, often unequal at a node, petiolate; laminae linear to orbicular, entire. Inflorescences of fasciculate or solitary flowers in the axils of leaves, sessile or pedicellate, often forming congested verticels; flowers bisexual, radially symmetrical, small and inconspicuous, perianth of 1 whorl but sometimes with petaloid staminodes, sepals (tepals) 5, thin and stiff, free, staminodes 0–20, often divided apically; stamens 3–30, free, filaments slender and borne from the base of perianth; ovary superior, 3- to 5-locular, with numerous ovules on axile placentae, styles short 3–5. Fruit a loculicidal capsule breaking into 3–5 thin-walled valves; seeds numerous and reniform, smooth or granulate, borne on slender funicles, strophiolate.

A genus of six to 10 species, four native to Africa and only one in our area. These small diffuse herbs are easily mistaken for members of the Caryophyllaceae.

***Glinus radiatus*** (R. & P.) Rohrb., in Mart., Fl. Bras. 14, pt. 2:238, pl. 55, f. 1. 1872. *Mollugo radiata* Ruiz & Pavon, Fl. Peruv. 1:48. 1798. Figure 42.

Herbs, prostrate or ascending, to 50 (80) cm tall, bisexual, leafy internodes 0.5 cm long, 0.3–2 (3.5) mm thick (dry), densely to sparsely puberulent with thin whitish stellate hairs. Leaves opposite or whorled, often unequal, petioles 1–5 (12) mm long, with lateral ridges continuous with the lamina margins; laminae 2–15 (30) mm long, 2–15 mm broad, elliptic to obovate or spatulate, usually broadest above the middle, obtuse or rounded at the apex, obtuse to cuneate at the base, margins entire and decurrent on the petiole, sparsely to densely puberulent with stellate whitish or grayish white hairs to 1 mm broad, venation pinnate with 1–3 pairs of major secondary veins. Flowers clustered in the leaf axils, sessile, or subsessile, densely or sparsely puberulent, perianth parts 4–4.5 mm long, greenish, with a short slender distal extension ca. 0.7 mm long. Fruit ca. 4 mm long and 2 mm thick, subtended and enclosed loosely by the persisting perianth; seeds many, 0.3–0.4 mm broad, reniform, smooth and bright reddish brown, lustrous.

A small weedy plant of open sites and often found on muddy river banks, road sides, cultivated fields and thickets in the Pacific lowlands (0–600 m) of Central America. Though the species is said to be common in the wet season, we have very few collections from Central America, and those were mostly made in the dry season; flowering material has been collected in April and June. The species ranges from Mexico to central Costa Rica and from the West Indies to South America.

*Glinus radiatus* is recognized by its small habit, opposite or whorled leaves, thin-branched stellate hairs, inconspicuous flowers tightly clustered in the leaf axils, and minute shiny reddish brown seeds. I have seen only a single collection from Costa Rica: Brenes 3872 from "Los Liros." These plants are very similar to some species of Caryophyllaceae.

#### MOLLUGO Linnaeus

Herbs, annuals or short-lived perennials, stems usually slender and much branched, often prostrate, not conspicuously succulent, glabrous; stipules minute or absent, deciduous. Leaves usually in whorls, rarely opposite, often beginning with a basal rosette; laminae simple and entire, usually broadest above the middle (often very narrow), glabrous. Inflorescences cymose or of solitary axillary flowers forming verticels at each node, pedicellate; flowers small, radially symmetrical, bisexual, perianth of 1 whorl of 5 equal or subequal tepals (sepals), imbricate in bud, free to the base; stamens 3–5 (rarely 6–10); ovary 3- to 5-locular, superior, ovules usually numerous on axile placentae, styles 3–5, short and slender. Fruit a thin-walled loculicidal capsule, breaking into 3–5 valves; seeds few to many, reniform to cochleate, embryo curved.

A genus of about 20 species, mostly in Africa and Asia, ranging from the tropics and subtropics into the temperate zone. These plants are very similar in

appearance to some of our species of Caryophyllaceae. Only one species is found in Central America.

***Mollugo verticellata* L., Sp. Pl. 89. 1753. Figure 41.**

Herbs, annuals to ca. 0.5 m tall, prostrate or erect, with much-branched slender stems, leafy internodes 1–9 cm long, 0.2–1 mm thick (dry), glabrous; stipules absent. Leaves 4–6 at a node in whorls or pseudowhorls (by condensation), variable in length and shape (often on the same plant), petioles 1–4 mm long and little differentiated from the lamina, slightly expanded at the base; laminae 5–30 (50) mm long, 0.5–4 (10) mm broad, linear to narrowly oblanceolate, broadest above the middle in larger leaves, acute at the apex, tapering gradually into the petiole, margins entire and continuous with the lateral margins of the petiole, glabrous and smooth, venation pinnate but usually obscure. Inflorescences verticel-like with 3–6 flowers in the axils of leaves (at a node), pedicels (3) 5–15 mm long, very slender (0.1–0.3 mm) and glabrous; flowers 2–3 mm long, white, perianth parts 2–2.5 mm long, 0.5–0.8 mm broad; stamens 3, to 2 mm long; ovary 3-locular, 1–1.5 mm long, styles 3. Fruit a loculicidal capsule subtended by the persisting perianth parts, 2.5–3 mm long, ovoid, thin-walled; seeds 20–30 per capsule, ca. 0.5 mm broad, cochleate to reniform, ridged along the curved back, dark reddish brown, lustrous.

Plants of open early secondary growth; often found on sandy sites along streams and in cultivated fields. *Mollugo verticellata* ranges from sea level to 500 (rarely 1,000) m elevation on both the Pacific and Caribbean slopes in Central America; flowering throughout the year, but with very few collections made in August and September. This species has a pantropical distribution, but appears to be uncommon in southern Central America.

*Mollugo verticellata* is recognized by its diffuse herbaceous habit, slender stems, verticels of narrow leaves, and small flowers on slender petioles. This species has been called *Clavellina montés* in El Salvador, according to Standley. It is easy to mistake this species for members of the Caryophyllaceae, such as *Arenaria lanuginosa* and *Spergula arvensis*, but these plants are restricted to higher elevations in Central America.

**SESUVIUM Linnaeus**

Herbs or subshrubs, prostrate to decumbent or erect, often rooting at the nodes, bisexual, glabrous, stems succulent; stipules absent. Leaves opposite, subopposite or alternate, simple and succulent, sessile or petiolate, clasping or sheathing at the base with the leaf bases of opposing leaves united across the node; laminae entire, linear to ovate. Inflorescences of solitary axillary flowers, sessile or pedicellate, subtended by 2 minute bracteoles; flowers bisexual, radially symmetrical, perianth of 1 whorl (sepals or tepals) united at the base to the floral cup (calyx cup), 5-parted, triangular, imbricate in bud, with a dorsal (abaxial) distal appendage; stamens 5–15 or many, filaments free or united at the base, borne on the floral cup; ovary superior and with 2–5 locules, ovules usually many on axile placentae, styles 2–5, slender. Fruit a circumscissile capsule, the apical lid coming off as a single unit; seeds several to many, black, cochleate to annular or reniform.

A genus of about six species: one a pantropical plant of the seashore, one endemic to the Galapagos Islands, and several restricted to eastern Africa.

***Sesuvium portulacastrum* (L.) L., Syst. Nat. ed. 10:1058. 1759. *Portulaca portulacastrum* L., Sp. Pl. 446. 1753. Figure 39.**

Herbs, perennial, prostrate or suberect, often creeping and rooting at the nodes and much branched, occasionally forming mats, stems thick and succulent, leafy internodes (0.5) 3–50 (80) mm long, 1–5 mm thick (dry), glabrous; stipules absent but the opposing leaf bases sheathing the stem and united. Leaves opposite, simple, petioles 2–6 mm long but not clearly differentiated from the lamina, with broad thin sheathing base; laminae 1–7



cm long, 1.5–8 (14) mm broad, linear to oblanceolate, obtuse or rounded at the apex, margin entire and gradually decurrent on the petiole, smooth and glabrous, succulent and bright green or reddish in life but drying dark and coriaceous, venation usually obscure. Flowers solitary in leaf axils, glabrous, pedicels 3–10 (15) mm long, ca. 1 mm thick, flowers 7–12 mm long, perianth lobes ca. 5 mm long and unequal, with a thickened central area and thin lateral margins, greenish on the outside and pink to reddish on the inside, with a short (1–1.5 mm) stiff appendage on the back (abaxial) distally, floral cup ca.  $\frac{1}{3}$  the length of the perianth lobes; stamens numerous and free, filaments 1.5–3.5 mm long, anthers 0.5–0.8 mm long; ovary 3–4 mm long, 3-locular (rarely 2 or 4), styles 3 or 4. Fruit 5–11 mm long and 5–6 mm thick, opening by a circumscissile slit, the perianth lobes persistent; seeds 8–30, black and smooth, 0.5–1.5 mm broad, reniform-cochleate.

Sprawling succulent plants usually found on or near sea beaches, occasionally found in salt flats and on open sandy or rocky sites from sea level to about 50 m elevation. Probably flowering throughout the year in Central America, but collected primarily from December through March and June through August. This species is pantropical, but appears to be uncommon in southern Central America.

*Sesuvium portulacastrum* is recognized by its succulent parts, narrow opposite leaves sheathing the stem at their base and united across the stem, solitary bright pink flowers with many stamens, and capsules opening by a circular slit. These plants are rarely found far from the seashore. The species has served as a vegetable, either eaten raw or cooked as greens. Superficially, this species resembles *Philoxerus vermicularis* of the Amaranthaceae, with small flowers in whitish spikes.

### TRIANTHEMA Linnaeus

Herbs or subshrubs, annual or short-lived, prostrate to erect, stems succulent, bisexual, glabrous or puberulent; stipule-like developments sometimes present on the united interpetiolar sheathing leaf bases. Leaves opposite or subopposite, simple, the opposing leaves at a node often unequal, petioles expanded at the base and clasping or sheathing the stem; laminae linear to orbicular, entire, succulent or semisucculent. Flowers solitary or fasciculate in leaf axils, sessile or pedicellate, sometimes united to the leaf base, radially symmetrical, bisexual, perianth united at the base to form a perianth tube (floral cup or calyx tube), 5-lobed, lobes often with a distal abaxial (dorsal) appendage; stamens 5 or 10 to many, borne on the edge of the perianth tube, alternate with the perianth lobes when of the same number, filaments free; ovary superior, 1-locular, ovules 2 to many on a parietal placenta, apex of the ovary truncate or depressed around the style, style 1, linear. Fruit a circumscissile capsule, seeds cochleate-reniform, with a rough or ridged surface.

A genus of nine species: one pantropical, one in Argentina, and the others in Africa, Asia, and Australia.

#### *Trianthema portulacastrum* L., Sp. Pl. 223. 1753. Figure 39.

Herbs, annual, prostrate to decumbent or erect, to 50 cm tall or 1 m long, bisexual, succulent, often reddish in color, often with alternate branching from the axil of the smaller leaf of a node, leafy internodes 0.5–10 cm long, 0.5–3.5 mm thick (dry), glabrous or with a single longitudinal ridge bearing slender crooked hairs on younger parts; sheathing leaf bases of opposing leaves united across the node and with a triangular stipule-like appendage to 3 mm long borne on the interpetiolar portion of the sheath. Leaves opposite or subopposite, the leaves of each node usually very different in size (the smaller often half the size of the larger), petioles 2–20 (30) mm long, conspicuously expanded at the base to form a thin sheathing base united with that of the opposing leaf and encircling the stem; laminae 1–4 (7) cm long, 0.5–2 (6) cm broad, broadly elliptic to spatulate in smaller leaves, to broadly obovate or suborbicular, larger leaves abruptly rounded at the apex and often

apiculate or emarginate, cuneate to obtuse at the base, margin entire, drying stiffly chartaceous to subcoriaceous, smooth and glabrous, with 2–4 pairs of major secondary veins. Flowers solitary and sessile in the leaf axils, bisexual, ca. 5–8 mm long, perianth tube campanulate, perianth lobes ca. 1.5 mm long and 1 mm broad; stamens 10, arising from the apex of the perianth tube (floral cup), filaments 1.5 mm long, anthers 0.5 mm long; ovary 1 mm long, irregularly lobed at the apex, style 1. Fruit a capsule surrounded by the persistent perianth tube and hidden within the sheathing leaf bases, ca. 5 mm long, 4 mm thick, crested at the apex, with circumscissile dehiscence at the middle; seeds 2–12, 1.5–2 mm broad, reniform-cochleate, reddish brown to black, with a rough surface.

Plants of open disturbed sites, from sandy sea beaches to cultivated ground and roadsides; ranging in altitude from sea level to 1,200 m, but rarely encountered above 500 m elevation in our area. Flowering primarily in the wet season, from June to December, but flowering collections have been made throughout the year in Central America. The species is pantropical, but has not been collected along the Caribbean coast in southern Central America.

*Trianthema portulacastrum* is recognized by the succulent stems, unequal opposite leaves with united sheathing leaf bases, and small pink flowers barely exerted beyond the sheathing leaf bases. This species has been called *Verdolaga* in Guatemala, according to Standley. The flowers are often difficult to see in pressed collections, since they are hidden by the sheathing leaf bases and are adnate, in part, to the petioles.

## PORTULACACEAE

Herbs or subshrubs (rarely shrubs), bisexual, usually with succulent stems, glabrous or puberulent at the nodes; stipules present or absent, often represented by scarious, fimbriate or tufted developments at the node. Leaves alternate, opposite, or condensed and basal or pseudovorticellate, simple, sessile or petiolate, the laminae usually thick-succulent, glabrous and entire, often small. Inflorescence terminal or axillary, paniculate, racemose, cymose or the flowers solitary; flowers bisexual (rarely unisexual), radially symmetrical, often small but brightly colored, perianth generally interpreted to be of 2 dissimilar whorls, sepals 2 (rarely 4–8), imbricate, free or united at the base, scarious or herbaceous, persistent or caducous, usually greenish (sepals sometimes interpreted to be floral bracts), petals 4 or 5 (6–18), free or united at the base, quickly wilting or rarely persisting, white to yellow or red; stamens 4 or 5 to many, often as many as the petals and opposite them, usually borne on a short floral cup, filaments free or united into fascicles, anthers 2-theous, dehiscing longitudinally; pistil 1, ovary superior (half-inferior to inferior in *Portulaca*), at first with locules and axile placentation but becoming unilocular at maturity and with basal placentation, ovules (1) 2 to many, campylotropous, styles 1–9, united near the base or free. Fruit usually a capsule, opening by loculicidal or circumscissile dehiscence (rarely a nut); seeds (1) 2 to many, slightly flattened, reniform to cochleate, embryo curved or folded.

A family of about 20 genera and 500 species, best represented in open sunny habitats in the seasonally dry tropics and subtropics. The family is closely related to Aizoaceae (especially *Sesuvium*) and exhibits similarities of ovary structure to that of the Caryophyllaceae. Our species are characterized by their generally small stature, fleshy stems and leaves, flowers subtended by two greenish sepals, four or more colorful petals, fruit that begin to open by a circumscissile slit, and the dark cochleate seeds borne on a basal placenta.

- 1a Plants with the leaves all condensed at the apex of a single thick rootstock, leafy internodes not visible, leaves linear (1.5–3 mm broad and up to 7 cm long); plants found only on the highest paramo, above 3,200 m elevation. . . . . *Lewisia*
- 1b Plants with conspicuous aerial stems and internodes, leaves rarely linear; not known to grow wild above 2,000 m elevation . . . . . 2a

- 2a Ovary partly or wholly inferior, fruit opening by a circumscissile slit at the middle or near the top; flowers sessile or subsessile and subtended by a cluster (involucre) of leaves; stems usually with tufts of hairs or cilia at the nodes (stipules) . . . *Portulaca*
- 2b Ovary superior, fruit opening irregularly; flowers borne on slender pedicels in an open panicle, not subtended by leaves; stems and leaves lacking stipules, glabrous  
*Talinum*

### LEWISIA Pursh

Herbs, perennial, aerial stem very short from a thick fleshy rootstock, rootstock simple or branched. Leaves mostly in a condensed basal cluster at the apex of the rootstock, simple and entire, somewhat succulent. Inflorescences racemose, paniculate or solitary and axillary, often subtended by leaflike bracts; flowers bisexual, radially symmetrical, sepals 2–8, persistent in fruit, petals 4–18, white to pink or red; stamens 5 to many; pistil 1, ovary superior, placenta basal and central, styles 3–8 and fused near the base. Fruit a thin-walled capsule, dehiscence circumscissile near the base and then splitting upward; seeds 6 to many, ovate to cochleate, smooth and lustrous.

A genus of 20 species of the southwestern mountains of the United States; one species extends southward on the tops of the highest mountains through Mexico to Guatemala and has recently been reported from the Chirripó páramo in Costa Rica. Species of this genus are often planted as ornamentals in rock gardens.

***Lewisia megarhiza*** (Hemsl.) MacBryde, J. Scott. Rock Gard. Club 13:295. 1973. *Calandrinia megarhiza* Hemsley, Diagn. Pl. Nov. 23. 1879. *Oreobroma mexicanum* Rydberg, N. Amer. Fl. 21:326. 1932. *O. megarhiza* (Hemsl.) Standl. & Steyererm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23:49. 1944.

Herbs, perennial, the short aerial stem and congested leafy internodes from the top of a single thick fleshy taproot to 10 cm long and 5–18 mm thick. Leaves all basal and congested at the apex of the taproot, simple and sessile; laminae 2–7 cm long, 1.2–3 mm broad, linear and entire, expanded near the base with thin sheathing margins, fleshy, glabrous. Flowers solitary on axillary pedicels 5–20 mm long, sepals 2, 6–7 mm long, petals 4–6, ca. 1 cm long, white. Fruit an ellipsoid capsule ca. 7 mm long and 4 mm thick, with very thin translucent walls; seeds numerous, 1.5 mm broad, cochleate, black, smooth and lustrous.

This species has been collected by Arthur Weston on Costa Rica's highest mountain, Chirripó Grande. All the specimens seen from Mexico and Guatemala were collected above 3,500 m elevation. The large taproot for so small a plant, the succulent linear leaves, the presence of only two sepals, and the distinctive fruit and seeds easily distinguish this species.

### PORTULACA Linnaeus

By Donna Ford and William Burger

REFERENCE: C. Diego Legrand, Desmembración del género *Portulaca*, I and II, Comun. Bot. Mus. Hist. Nat. Montevideo vol. 3, no. 31:1–15, 1953 and no. 34:1–17, 1958.

Herbs, annual or perennial, often prostrate, stems succulent glabrous or puberulent; stipules often reduced to a ridge with conspicuous hairs. Leaves alternate, subopposite or crowded and pseudoverticillate, simple and entire, sessile or petiolate, usually succulent and glabrous. Inflorescence of 1 to several flowers terminal on main and lateral stems, often subtended by closely crowded leaves forming an involucre; flowers bisexual and radially symmetrical, sessile or subsessile, perianth of 2 whorls, sepals 2, unequal and united near the base, petals 4–6, white, yellow or reddish, united only near the base, quickly with-

ering; stamens (4–6) 7 to many, borne on the base of the united corolla, filaments free; pistil solitary, ovary half-inferior to inferior, unilocular, ovules numerous on a basal placenta, styles 3–9 and united at the base. Fruit a circumscissile capsule, the top coming off as a single unit (calyptra), thin-walled; seeds usually numerous, cochleate to reniform, smooth to minutely tuberculate.

A genus of 150–200 species, distributed widely in tropical and subtropical regions. The small stature, succulent stems, brightly colored flowers subtended by an "involucre" of congested leaves, and calyptrate thin-walled fruit with cochleate seeds are distinctive. The genus is well represented in Mexico, and a number of species range southward to Guatemala and Honduras.

- 1a Leaves usually more than 4 mm wide, laminae flat; axillary hairs absent or inconspicuous (to 1 mm long).....2a
- 1b Leaves usually less than 4 mm wide, laminae often terete; axillary hairs present and conspicuous, 1–18 mm long.....3a
- 2a Ovary superior to half-inferior; capsule not winged, circumscissile at the middle or below, operculum hemispherical; seeds black, brown or blue-waxy; flowers yellow .....*P. oleracea*
- 2b Ovary half-inferior to inferior; capsule with a circular wing, circumscissile at the middle or above, operculum flat or slightly rounded; seeds gray at maturity; flowers yellow to red .....*P. umbraticola*
- 3a Petals less than 1 cm long, pink to purple; stamens fewer than 40; small plants of open weedy sites .....*P. pilosa*
- 3b Petals more than 1 cm long and the flowers more than 2 cm broad, variously colored; stamens more than 40; cultivated ornamentals and not naturalized in Costa Rica; *P. grandiflora* Hooker.

**Portulaca oleracea** L., Sp. Pl. 445. 1753. *P. marginata* H.B.K., Nov. Gen. & Sp. 6:58. 1823. Figure 39.

Herbs, prostrate or ascending, often with many branches radiating from a single base, stems succulent and often becoming reddish, leafy internodes 0–5 cm long, 0.5–3 mm thick (dry), glabrous except at the nodes; stipules present in the form of a minute ridge with slender whitish hairs to 1 mm long (just below the leaf base). Leaves alternate to subopposite and opposite, often crowded together at the ends of branches; petioles 0.5–4 (8) mm long, expanded at the base with thin lateral margin; laminae 0.4–4 cm long, 0.3–2 cm broad, spatulate to obovate or obtriangular, bluntly rounded at the apex, tapering gradually to the cuneate base, margins entire and decurrent on the petiole, smooth and glabrous, succulent but drying dark and stiffly chartaceous, venation obscure. Flowers sessile at the ends of branches, solitary or clustered together, subtended by a cluster of leaves, hairs at the base of the flower inconspicuous, with a short floral cup (perianth tube), sepals 2, broadly ovate, 3–4.5 mm long, petals 4–6, 3–4.5 mm long, bright yellow; stamens 6–15, filaments ca. 1.6 mm long; style with 4–6 branches. Fruit ovoid, 4–8 mm long, 3–4 mm thick, circumscissile below the middle, distal cap 2–4 mm long; seeds 0.6–1 mm broad, cochleate, black, with granular or minutely tuberculate surface.

Plants of open sunny sites, often found along roadsides, on sand and gravel bars along streams, and in open weedy fields from sea level to 1,500 (2,000) m elevation on both the Caribbean and Pacific sides of Central America. The species appears to flower throughout the year, but is most commonly encountered from October to March. This species has become established all over the world, in both tropics and subtropics.

*Portulaca oleracea* is recognized by its small stature, numerous glabrous stems, succulent little leaves often crowded at the ends of stems and forming an involucre beneath the sessile yellow flowers, and the circumscissile fruit with basal placentation. The distal flowers on main stems and lateral stems with terminal flower clusters often form cymelike arrangements. These plants are called



*Verdolaga* in Central America ("Purselane" in English) and are often cooked as a vegetable.

***Portulaca pilosa* L., Sp. Pl. 445. 1753. Figure 41.**

Herbs, prostrate or erect, stems succulent, rarely exceeding 20 cm in length, leafy internodes 0–2 cm long; intrapetiolar stipule present, with tufts of whitish hairs 3–10 mm long from a band of tissue ca. 1.5 mm broad just above the leaf base. Leaves alternate or crowded together, sessile or with a short (1 mm) petiole; laminae 0.5–2 cm long, linear to narrowly lanceolate, acute at the apex, gradually narrowed at the base and decurrent on the petiole, margins entire, the laminae succulent (often terete) in life and glabrous, drying dark, venation obscure. Flowers sessile and crowded at the ends of stems, 2.5–3 mm long, subtended by a cluster of leaves forming an involucre, sepals 2–3 mm long, petals 3–5.5 mm long, reddish or purple; stamens 15 to many, filaments red. Fruit a circumscissile capsule, 3–4 mm in diameter; seeds 0.5–0.7 mm broad, slightly flattened, cochleate in outline, minutely tuberculate, black.

Plants of open sunny sites and often found on rocky sites or sand along streams from near sea level to 1,200 m elevation along the Pacific slope of Central America and in the Caribbean lowlands; flowering primarily from June to February. The species ranges from the southeastern United States, the West Indies, and Mexico through Central America to South America.

*Portulaca pilosa* is characterized by its small succulent stems with unusual fimbriate intrapetiolar stipules that give a tufted white-hairy appearance to the stems. The distal rose red flowers subtended by similar tufted hairs and by a cluster of leaves are also distinctive. The species has only been collected in the seasonally very dry areas of the northern Pacific slope in Costa Rica, during the wet season.

***Portulaca umbraticola* H.B.K., Nov. Gen. & Sp. 6:72. 1823. *P. lanceolata* Engelm., Boston J. Nat. Hist. 6:154. 1850, non Haw. 1803. *P. coronata* Small, Bull. Torrey Bot. Club 23:126. 1896. *P. plano-operculata* Kuntze, Rev. Gen. 3:16. 1898. *P. denudata* Poellin., Repert. Spec. Nov. Regni Veg. 33:159. 1933.**

Herbs, 10–50 cm tall, annual, stems prostrate to erect and simple or with open branching, stems glabrous and green to magenta, roots fibrous; stipules absent or represented by short (1 mm) whitish hairs at the axils. Leaves alternate along the stems and in whorls of 3–8 beneath the flowers, subsessile or with short (1–2 mm) petioles; laminae 1–3 (5) cm long, 0.4–1.1 (1.6) cm broad, lower laminae spatulate to obovate, the upper oblanceolate to oblong, usually rounded at the apex, tapering gradually to the base, glabrous, succulent, venation obscure. Flowers in terminal clusters, bracteoles 1.5–2 mm long, lanceolate to deltoid; sepals 2, 3–5 (8) mm long, ovate, petals to 1 cm long, yellow to orange or red, spatulate or obovate; stamens 7–27, anthers narrow; ovary with an adnate corona, style 5–8 mm long, stigmatic branches 3–8. Fruit a capsule subtended by the persisting leaves and calyx, 3–5 mm long, usually turbinate, sessile or borne on a pedicel to 4 mm long, circumscissile at the middle or above, the operculum rounded, 3–4 mm broad and 1–2 mm high, the coronal wing 0.5–1 mm wide, arising just below the line of dehiscence; seeds 0.7–1 mm broad, gray, cochleate and tuberculate.

Plants of open sunny sites in seasonally dry areas, ranging from near sea level to 1,200 m in our area, but rarely collected below 600 m in central Central America. Flowering material has been collected from June to September in Central America, along the Pacific slope, and in the Central Highlands. The species ranges from the southern United States (Arizona to Georgia), Mexico, and the West Indies through Central America to South America.

*Portulaca umbraticola* is recognized by its succulent and glabrous stems and

leaves (hairs only at the leaf axils), the terminal flowers subtended by a whorl of leaves, fruit opening by the circumscissile dehiscence of a slightly domed (curved) lid or operculum, and the restriction to seasonally very dry vegetation. This species has only recently been collected in Costa Rica at the Santa Rosa National Park in Guanacaste province (*Liesner & Lockwood 2687*). While common in Honduras between 600 and 1,100 m elevation, we have not seen specimens from Guatemala. In Honduras the species is called *Verdolaga*.

### TALINUM Adanson

Herbs or subshrubs, annual or perennial, bisexual, stems often succulent, usually glabrous; stipules absent. Leaves alternate or subopposite, simple and entire, usually quite succulent. Inflorescences often cymose, the cymes arranged in compound panicles or simple and few flowered, flowers rarely solitary and axillary, usually pedicellate; flowers bisexual, radially symmetrical, sepals 2, opposite and free, usually early deciduous, petals 5 or more, free or connate at the base, deciduous; stamens 5 to many, sometimes united into antipetalous fascicles, filaments slender; pistil 1, ovary superior, 1- or 3-locular near the base, placentation basal or free central, styles 3, united near the base. Fruit a capsule, 1- or 3-locular near the base, opening from the top into 3 valves or irregularly; seeds somewhat flattened, cochleate to reniform in outline.

A genus of probably fewer than 50 species, two of which are found in Central America. The genus ranges from temperate and tropical America to Africa and Asia.

- 1a Plants with succulent stems that do not persist through the dry season; larger leaves 3–6 cm broad; inflorescence a much-branched panicle with many distant flowers; sepals 3–4 mm long; uncommon plants of the seasonally dry Pacific slope from Mexico to Costa Rica ..... *T. paniculatum*
- 1b Plants with woody stems that persist through the dry season and are perennial; larger leaves rarely exceeding 2.5 cm in breadth; inflorescence a few-branched cyme or raceme; sepals 5–6 mm long; ranging from Mexico to central Nicaragua and not included in the descriptions: *T. triangulare* (Jacq.) Willd. (See note below.)

***Talinum paniculatum* (Jacq.) Gaertner**, *Fruct. & Sem.* 2:219, pl. 128, f. 13. 1791. *Portulaca paniculata* Jacquin, *Enum. Pl. Carib.* 22. 1760. *P. patens* L., *Mant. Pl.* 242. 1771. *T. patens* (L.) Willd., *Sp. Pl.* 2:863. 1800. *Claytonia paniculata* (Jacq.) O. Ktze., *Rev. Gen.* 1:57. 1891. Figure 40.

Herbs, erect to 1 m tall, stems succulent and simple or with a few lateral branches, from a tuberous base, glabrous, leafy internodes 0.5–10 cm long, 1–6 mm thick; stipules absent. Leaves alternate, glabrous, petioles 1–15 mm long and not clearly differentiated from the lamina, with lateral wings continuous with the lamina margins; laminae 2–13 cm long, 1–6 cm broad, elliptic to obovate, abruptly obtuse or rounded at the apex, tapering gradually to the cuneate base and decurrent on the petiole, margins entire, succulent in life but drying brittle (chartaceous to subcoriaceous) and dark, the 2–4 pairs of major secondary veins often obscure. Inflorescences 10–60 cm long, 6–20 cm broad, terminal, paniculate with a central stem and slender alternate branches, flowers in open cymes on very slender (0.2 mm, dry) pedicels 1–2 cm long; flowers 3–4 mm long, perianth of 2 whorls and not persisting in fruit, sepals ca. 2 mm long, petals ca. 3 mm long, yellow or pink; stamens 15 or more, filaments 1.2–2 mm long, anthers 0.3–0.5 mm long; ovary globose, 1 mm long. Fruit a lustrous yellowish globose capsule 3.5–5 mm in diameter, breaking open irregularly; seeds slightly flattened, cochleate in outline, 1–1.5 mm broad, surface black and lustrous, minutely reticulate, strophiolate.

Plants of open weedy sites, riverbanks, and thickets from (0) 100 to 1,200 m elevation along the seasonally very dry Pacific slope of Central America; growing and flowering in the wet season, from June to December. The species ranges

from the southern United States, Mexico, and the West Indies through Central America and Panama to South America.

*Talinum paniculatum* is recognized by its succulent alternate leaves on few-branched stems, open panicate inflorescences with slender stems, small flowers with only two sepals, and capsules opening irregularly to disperse small black snail-shaped seeds. These plants are rarely collected in Costa Rica and are probably confined to the northern half of the Pacific slope.

*Note added in proof:* *Talinum triangulare* (Jacq.) Willd. has recently been collected by Robert Wilbur near the railroad yards at Puerto Limon, where it appears to be a recent arrival.

## BASELLACEAE

Twining herbs or climbing subshrubs or vines, annual or perennial, bisexual, glabrous; without stipules. Leaves alternate and simple, petiolate, often cordate, usually slightly succulent, entire and glabrous. Inflorescences axillary or terminal, spikes, racemes or panicles, glabrous, small slender bracts present at the base of the pedicels and with 2–4 sepeloid bracteoles; flowers small, bisexual or unisexual, perianth of a single whorl but often appearing to have 2 whorls because of the sepeloid bracteoles adnate to the base of the flowers, perianth petaloid and 5-parted, forming a tube or almost free to the base; stamens 5, opposite the perianth parts and borne at their base, filaments free, anthers versatile, dehiscing variously; pistil 1 with superior ovary, 1-locular with basal placentation, ovule solitary, short-stalked and campylotropous, style 1–3, stigmas separate or 3-lobed. Fruit an indehiscent utricle, enclosed by the often fleshy perianth or winged bracteoles (winged sepals of some authors); seeds solitary, small, spherical or flattened.

A small tropical family of five genera. *Anredera vesicaria* (Lam.) Gaertn., with fruit bearing wings 4 to 5 mm long, is found in northern Central America. *Ullucus tuberosa* Lozano, with potato-like tubers, is an important food plant in the Andean region of South America. *Basella alba* L. of the Old World tropics is cultivated for its fleshy leaves which serve as an excellent spinach-like vegetable. None of the aforementioned species has been reported in Costa Rica, but *Basella alba* is cultivated in central and eastern Panama (see treatment of the family in the Flora of Panama, Ann. Missouri Bot. Gard. 66:109–115, 1979). The family is closely related to the Portulacaceae.

## BOUSSINGAULTIA Humboldt, Bonpland, and Kunth

Vines or herbaceous twiners with slender distal stems, bisexual, glabrous, often succulent; stipules absent. Leaves alternate and simple, petiolate, slightly succulent, often becoming cordate in larger leaves. Inflorescences axillary or terminal, racemes or panicles, flowers subtended by slender bracts and with 2 sepal-like bracteoles at the apex of the pedicel; flowers bisexual and radially symmetrical, perianth of 5 petaloid parts whitish but often turning dark when dry, the sepeloid bracteoles united to the base of the corolla-like perianth tube; stamens borne on the base of the corolla tube, inflexed in bud, filaments slender, anthers versatile; ovary ovoid, style 1 with 3 stigmas or the style with 3-lobed stigma. Fruit a utricle enclosed within the persisting perianth; seed solitary erect.

A genus of about 10 species in tropical America. Three species are found in northern Central America, but only one of these species has been recorded from Costa Rica.

***Boussingaultia ramosa*** (Moq.) Hemsley, Biol. Centr. Amer. Bot. 3:27. 1882. *Tandonia ramosa* Moq., in DC., Prodr. 13, pt. 2:227. 1849. *Dioscorea calyculata* Donnell Smith, Bot. Gaz. 20:295. 1895. Figure 40.



FIG. 39. Caryophyllales: succulent species with opposite leaves usually clasping the stem at their base. Aizoaceae: species of *Sesuvium* and *Trianthema*. Amaranthaceae: *Philoxerus vermicularis*. Portulacaceae: *Portulaca oleracea*.





FIG. 40. Caryophyllales: a climber and an erect herb, both with semisucculent leaves. Basellaceae: a species of *Boussingaultia*. Portulacaceae: a species of *Talinum*.

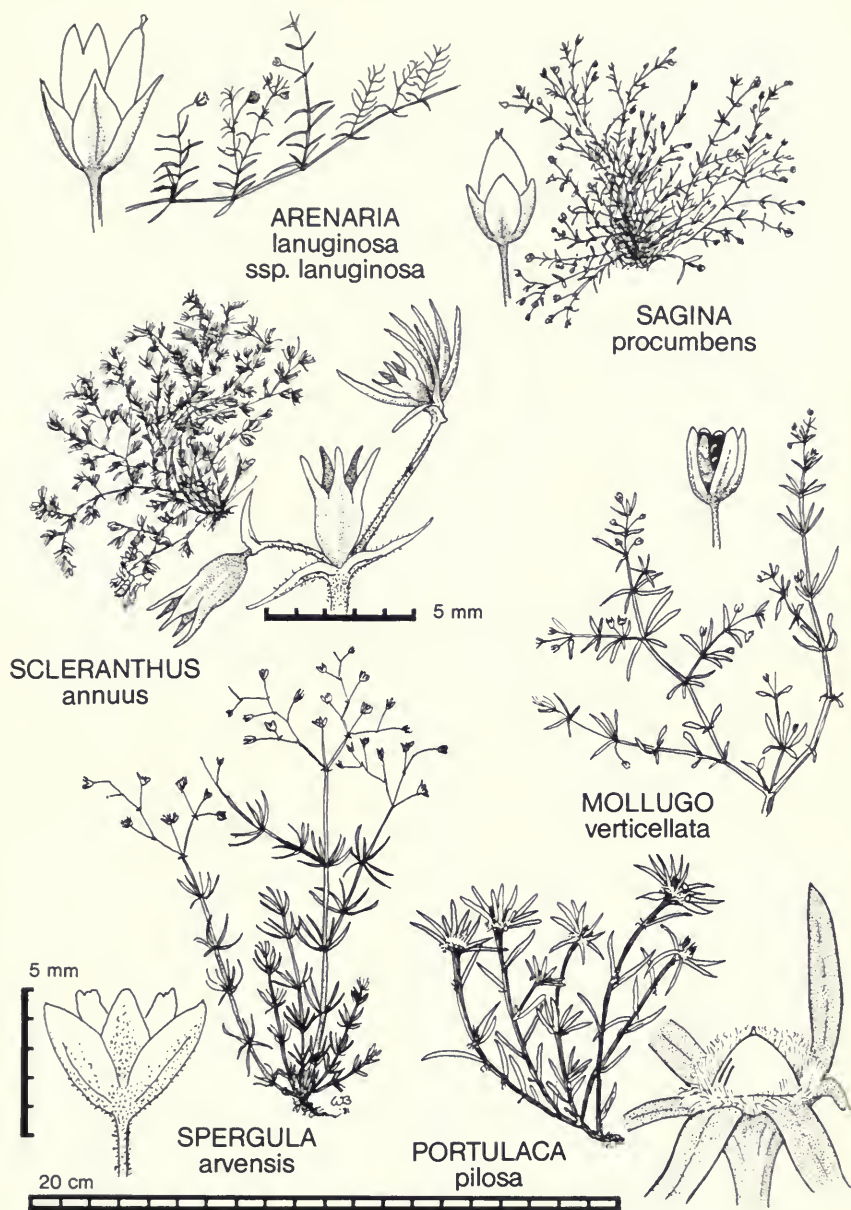


FIG. 41. Caryophyllales: herbs with narrow opposite leaves. Aizoaceae: *Mollugo verticellata*. Portulacaceae: *Portulaca pilosa*. Caryophyllaceae: species of *Arenaria*, *Sagina*, *Scleranthus*, and *Spargula*.

**ARENARIA**  
*lanuginosa*  
ssp. *guatemalensis*,



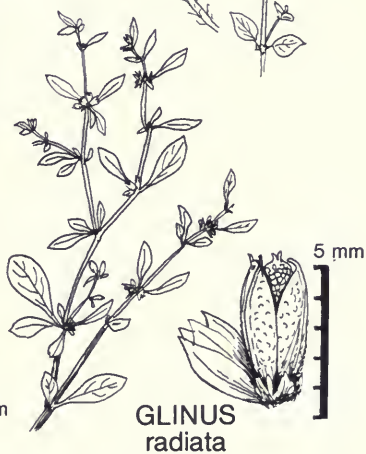
**STELLARIA**  
*ovata*



**DRYMARIA**  
*cordata*



**CERASTIUM**  
*guatemalensis*



**GLINUS**  
*radiatus*

FIG. 42. Caryophyllales: species with broader opposite or whorled leaves. Aizoaceae: *Glinus radiatus*. Caryophyllaceae: species of *Arenaria*, *Cerastium*, *Drymaria*, and *Stellaria*.

Herbaceous or woody climbers, annual or perennial, distal stems often pendulous, glabrous, leafy internodes 2–6 cm long, 1–4 mm thick; stipules absent. Leaves alternate in a spiral, distant, glabrous, petioles 6–25 mm long, sulcate above with 2 adaxial ridges continuous with the lamina margins; laminae 2–6 cm broad, broadly ovate, acute to obtuse at the apex and with a mucronate tip ca. 3 mm long, obtuse to truncate or cordate (in larger leaves) at the base, margins entire and decurrent on the petiole, somewhat succulent in life but drying thin-chartaceous or membranaceous, venation pinnate or subpalmate with 2 or 3 pairs of major secondary veins, smooth and glabrous. Inflorescences slender open racemes borne on leafless paniculiform axillary or terminal branches, 6–35 cm long, rachis 0.2–0.6 mm thick (dry) and glabrous, with slender linear-lanceolate bracts subtending the pedicels ca. 2 mm long, pedicels ca. 1.5 mm long; flowers ca. 2 mm long, subtended by a pair of sepaloid bracteoles ca. 0.6 mm long, perianth petaloid, 2 mm long, broadly imbricate, whitish but becoming dark when dried, united and narrowed above the calyx-like bracteoles, ovary ca. 1 mm long, ovoid. Fruit apparently quickly caducous, usually enclosed by the dark perianth and pale-colored subtending bracteoles, with 2 lateral winglike developments at the base of the perianth ca. 1 mm long, fruit lustrous subglobose and with a small disk at the apex, ca. 0.7 mm long; seed difficult to extricate from the tightly enclosing fruit wall.

Plants of open thickets and climbing over others, from 700 to 2,000 m elevation along the Pacific slope of Central America; collections with flowers and fruit have been made from October to February. The species ranges from Mexico to Costa Rica.

*Boussingaultia ramosa* is characterized by its glabrous slender distal climbing stems with alternate slightly succulent leaves, the long pendulous racemes with little white flowers, the two sepaloid bracteoles at the apex of the pedicel, and the minute fruit with single seed. This species resembles some species of *Dioscorea* and Polygonaceae, but the five-parted perianth and estipulate leaves serve to place these slender climbers in their appropriate family.

## CARYOPHYLLACEAE

By Richard A. Baker and William C. Burger,  
with Cerastium by David Good

Herbs (rarely subshrubs or shrubs), annuals or perennials, plants bisexual (rarely unisexual), glabrous to densely puberulent, nodes often slightly thickened; stipules present or absent and then the leaf often with a clasping or sheathing base, interpetiolar ridges or sheaths sometimes present. Leaves simple and undivided, opposite or pseudoverticillate (rarely alternate), laminae usually entire. Inflorescences often cymose, loosely dichasial to compact and capitate, many to few flowered or the flowers solitary on distal stems, floral bracts or reduced leaves often subtending the pedicels, rarely with 1–3 pairs of bracts immediately subtending the calyx (called an epicalyx) as in *Dianthus*. Flowers bisexual (rarely unisexual), radially symmetrical, calyx of 5 or 4 free sepals or united to form a calyx tube with 5 (4) lobes or teeth, hypogynous or borne on a cupulate hypanthium, persisting in fruit and becoming dry and stiff; petals 5 or 4 (0), free, entire to deeply bilobed or serrate at the apex, white to pink or purple and red (the petals usually divided into a narrow petiole-like claw at the base and a distal expanded blade in genera with united sepals, the clawed petals often with small ligule-like appendages above the junction of claw and blade); stamens usually 10 in 2 whorls of 5, often fewer by reduction, often united at the base but the filaments free for most of their length, anthers 2-celled, dehiscing longitudinally; pistil solitary, often narrowed at the base or borne on a short stalk, ovary 1- to 5-locular, often with septa at the base and a single locule in the upper half, placentation axile, central, free-central or basal, ovules few to many (rarely solitary), styles 2–5, free or united at the base. Fruit usually a thin-walled capsule (1-seeded indehiscent utricle or berry-like in a few genera), often borne on a short stalk, usually breaking into as many septa as there are styles, capsules of flowers with united tubular calyx usually opening only at the top with small teeth; seeds usually reniform to cochleate or circular, often slightly flattened on 2 sides, smooth to tuberculate, with or without a small aril-like appendage



(strophiolate or estrophiolate); seeds usually with a curved embryo enclosing perisperm and little or no endosperm.

A family of about 75 genera which is most numerous in the cooler regions of the world and very poorly represented in the lowland tropics. A number of taxonomically difficult genera include species that have become cosmopolitan weeds; the names and status of these species will probably continue to give us difficulty for years to come. The family includes a number of ornamentals that are important both in gardens and in the cut-flower trade. These herbaceous plants can usually be recognized by their opposite simple and entire leaves, the separate petals often cleft or fimbriate at the apex, the thin-walled capsules, and the seeds usually reniform (kidney-shaped) to cochleate (snail-shaped).

- 1a Flowers with the sepals free or united only at the base (calyx-tube, calyx-cup or urceolate hypanthium absent); native and naturalized weedy plants, not grown for ornamental use ..... 2a
- 1b Flowers with the calyx united to form a cup or a tube, or the sepals borne on the apex of an urceolate hypanthium; introduced weeds or garden plants grown for their ornamental flowers and inflorescences ..... 8a
- 2a Stipules present at the leaf base (sometimes falling off early), leaf bases not clasping or sheathing the stem, interpetiolar lines often present ..... 3a
- 2b Stipules absent, leaf bases often clasping or sheathing the stem, an interpetiolar line or sheath often present ..... 5a
- 3a Leaves opposite and broad; styles united near the base; seeds cochleate and tuberculate; commonly encountered native plants ..... *Drymaria*
- 3b Leaves opposite or whorled or appearing to be whorled by condensation of short axillary shoots, leaves linear to narrowly obovate; rarely collected introduced weeds of higher elevations ..... 4a
- 4a Leaves linear and appearing to be whorled; styles free to the apex of the ovary; seeds subglobose and with a whitish circumferential margin or wing ..... *Spergula*
- 4b Leaves narrowly obovate or oblong-obovate, opposite or whorled; styles united for most of their length; seeds semicircular to subulate and without a margin or wing ..... *Polycarpon*
- 5a Capsule cylindrical and usually somewhat curved, opening by 10 short teeth; plants often conspicuously puberulent ..... *Cerastium*
- 5b Capsule ovoid and straight, opening by 2–8 teeth ..... 6a
- 6a Seeds reniform-globose, seed coat lustrous and smooth, maroon to black in color; petals entire; laminae often with a delicate submarginal vein along distal margins ..... *Arenaria*
- 6b Seeds usually cochleate with muricate to tuberculate surfaces, brownish and dull; petals entire to deeply 2-lobed ..... 7a
- 7a Petals entire; styles 4 or 5; leaves linear and less than 8 mm long, a submarginal vein absent ..... *Sagina*
- 7b Petals 2-lobed; styles usually 3; leaves usually ovate to cordate and the larger more than 8 mm long (*S. nubigena* has small lanceolate leaves but is very rare), a submarginal vein present or absent ..... *Stellaria*
- 8a Sepals narrow and borne at the distal rim of a small (1.5 mm) urceolate hypanthium, petals absent; leaves linear and rarely more than 12 mm long, with an interpetiolar sheath at the base; fruit with 1 seed; weeds (rare in Costa Rica) ..... *Scleranthus*
- 8b Sepals united for much of their length to form a tube or united halfway to form an open cup; petals present; fruit with numerous seeds; planted for ornament or an escaped weed with viscid glandular hairs in *Silene gallica* ..... 9a
- 9a Flowers less than 1 cm long, calyx united for half its length; styles 2 or 3; capsules 4-valved, 4–5 mm long; inflorescences open and diffuse, with many flowers on long slender pedicels; grown for ornament ..... *Gypsophila*
- 9b Flowers usually over 15 mm long, calyx united to form a tube with small apical teeth, calyx tube usually enclosing most of the fruit; capsules opening by small apical teeth, more than 5 mm long; inflorescences usually few-flowered ..... 10a

- 10a Styles 5 or 4; calyx 15–20 mm long; garden plants covered with grayish white tomentum ..... *Lychnis*  
 10b Styles 2 or 3; plants never covered with dense grayish white puberulence ..... 11a  
 11a Styles 3; calyx 6–16 mm long, with 10 or more thick distinct veins; capsule with 6 short apical teeth; glabrous and with showy flowers or a weed with glandular pubescence distally ..... *Silene*  
 11b Styles 2; calyx 15–24 mm long, with many veins, the veins not thickened; capsule usually with 4 apical teeth; glabrous garden plants ..... *Saponaria*

## ARENARIA Linnaeus

REFERENCE: J. McNeill, The delimitation of *Arenaria* and related genera in North America, with 11 new combinations in *Minuartia*. *Rhodora* 82:495–502. 1980.

Annual, biennial or perennial herbs, sometimes with a woody rootstock, stems diffusely branched, procumbent, repent or ascending and clambering, occasionally forming dense cushion-like mats, glabrous or puberulent; estipulate. Leaves opposite, sessile or very short petiolate, linear to narrowly elliptic or ovate, entire, usually clasping the stem at their base. Inflorescences dichasial, axillary or terminal, or the flowers solitary at the nodes (as in ours); flowers bisexual, radially symmetrical, small, sepals 5, free or only slightly united at the base, petals 5 (absent in *A. quirosii* and some northern subspecies of *A. lanuginosa*), white (in ours), free, apically entire to slightly emarginate or dentate; stamens 10, rarely 5, usually borne on a slightly elevated perigynous disk, anthers versatile, dehiscent longitudinally, 2-therous; ovary superior, unilocular, placentation basal with many ovules, styles usually 3 or 5 (occasionally 2 or 4), free. Fruit a capsule dehiscent by as many valves as there are styles, valves 1-lobed or bilobed at the apex, thin-walled, unopened fruit ovoid to globose or oblong; seeds often numerous, subglobose or slightly compressed, reniform to subcircular in outline, the surface smooth and lustrous (in ours) or rough and tuberculate, estriolate.

A genus of perhaps 200 species, primarily of seasonally cold habitats in the Northern Hemisphere. Two species occur in Costa Rica, one apparently endemic. The Costa Rican species of *Arenaria* can be distinguished from our other Caryophyllaceae by the combination of their dark maroon or black, smooth and shiny, reniform-globose seeds, the lack of stipules, the usually narrow leaves, the solitary axillary flowers borne on conspicuous slender pedicels, and the entire petals (when petals are present). The members of this genus have only rarely been collected below 1,000 m elevation in Costa Rica. One of our species is polymorphic and is here treated as a single species; see the discussion under *A. lanuginosa*.

- 1a Laminae less than 5 mm long, broadly ovate to obovate; flowers lacking petals; probably restricted to areas above 3,000 m elevation, rarely collected ..... *A. quirosii*  
 1b Laminae usually over 10 mm long (linear to lanceolate or narrowly elliptic-ovate when less than 10 mm long); flowers with petals but the petals deciduous; a polymorphic array of plants ranging from 700 to 3,400 m elevation ..... *A. lanuginosa*

*Arenaria lanuginosa* (Mich.) Rohrbach, in Mart., Fl. Brasil. 14, pt. 2:274. 1872, sensu lato. *Spergulastrum lanuginosum* Michaux, Fl. Bor. Amer. 1:275. 1803. *A. alsinoides* Willd. ex Schlecht., Mag. Ges. Naturf. Freund. Berlin 7:201. 1816. *A. nemorosa* H.B.K., Nov. Gen. & Sp. 6:35. 1823. *A. saxosa* A. Gray, Pl. Wright. 11:18. 1853. *A. guatemalensis* Standl. & Steyererm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23:50. 1944. *A. lanuginosum* ssp. *saxosa* (A. Gray) Maguire, Amer. Midl. Naturalist 49:498. 1951. *A. lanuginosa* ssp. *guatemalensis* (Standl. & Steyererm.) J. Duke, Ann. Missouri Bot. Gard. 48:93. 1961. Figures 41 and 42.

Herbs, prostrate, decumbent or clambering over other plants, to 1 m tall, perennial from a taproot, usually much branched from the base, bisexual, leafy internodes 0.2–5 (15) cm long, 0.3–2 mm thick, usually puberulent with slender whitish hairs 0.1–0.3 mm long, hairs often confined to longitudinal ridges. Leaves opposite, equal or subequal at each node, differing greatly in different plants but usually quite similar on the same plant, sessile or subsessile, petioles to 3 mm long; laminae 4–30 (40) mm long, 1–16 mm broad, linear to narrowly elliptic or elliptic-ovate, obtuse or acute at the apex, slightly (0.5 mm) mucronate at the tip, gradually narrowed at the base and clasping the stem, margins entire and often minutely ciliate; laminae drying thin-chartaceous, smooth and usually puberulent (especially on the midvein) with thin whitish hairs ca. 0.2 mm long, with a single prominent midvein, secondaries obscure. Flowers solitary and borne from the axils of distal leaves, pedicels slender, 0.5–4 cm long, usually puberulent, the flowers small, 3–6 mm long, sepals 2–5 mm long, usually with green center and translucent margins, acute at the apex, persisting in fruit; petals shorter or longer than the sepals, to 8 mm long, thin and whitish, usually deciduous; stamens shorter than or as long as the sepals, filaments 1–4 mm long; ovary ovoid. Fruit 2.5–6 mm long, ovoid-ellipsoid, valves 2–5, thin-walled and yellowish, splitting to the base or only halfway, thin-walled and yellowish; seeds 0.6–1 mm broad, slightly flattened, suborbicular to slightly cochleate in outline, reddish brown (in early stages) to lustrous black, surface usually smooth.

Horizontally spreading or clambering herbs in open sites and in moist forest understory of montane forest and highlands. The species is rarely found below 1,500 m elevation in Costa Rica, but ranges as low as 500 m in Guatemala; it can be found on our highest mountains, and flowering collections have been made throughout the year. The species ranges from the southern United States through Mexico and Central America to Peru and Brazil.

*Arenaria lanuginosa* (in a wide sense) is characterized by its opposite subsessile, narrow, little leaves, sprawling or clambering stems, solitary little flowers on thin pedicels arising from the axils of distal leaves, the biseriate perianth with undivided petals (in our area), and the thin-walled capsule with basal placenta.

The broad circumscription of this species avoids the problems of erecting new species, but such a treatment obscures what may be real differences between population groups in Central America. The following key was developed by Richard Baker and recognizes four species-like taxa in Costa Rica. Three are designated subspecies and are consistent with the treatment by James Duke in the Flora of Panama; the fourth is unnamed. This key seems to work effectively for a majority of the specimens encountered in Central America, but it may be ineffective elsewhere in the range of the species. There are occasional collections that seem to have intermediate characteristics, and this is consistent with the experience that others have had with other species of *Arenaria*. We do not know if the four entities separated by the key deserve specific rank as they were given in the Flora of Guatemala; we present this key in the hope that it will suggest further study.

- 1a Valves of the mature capsule not exceeding or only slightly exceeding the sepals; sepals glabrous, 3–4.5 mm long, petals as long as or longer than the sepals; laminae usually less than 2 cm long and 5 mm broad, ciliate along the margin only on the proximal half of the lamina; styles 2 or 3; plants found above 3,000 m elevation on Volcan Baru, Chiriqui, Panama ..... ssp. *saxosa*
- 1b Valves of the mature capsule usually exceeding the sepals; sepals usually puberulent ..... 2a
- 2a Petals longer than the sepals; styles usually 3, capsule valves more than 4.5 mm long; pedicels (1.5) 2–5 cm long; laminae to 4 cm long and often more than 5 mm broad; plants usually found only above 1,800 m elevation ..... ssp. *guatemalensis*
- 2b Petals equaling or shorter than the sepals; capsule valves shorter than 4.5 mm or, if longer, the pedicels 1.5 cm long or less; laminae rarely more than 2.5 cm long or 5 mm broad ..... 3a



- 3a Styles 2–4; capsule valves 2–4, usually bilobed and revolute, 3–4 mm long (rarely longer); sepals usually 2–3 mm long; 500–1,800 (2,400) m elevation. .ssp. *lanuginosa*  
 3b Styles 5; capsule valves 5, sometimes bilobed, usually entire and straight, 5–7 mm long; sepals 2.7–4 mm long; (1,800) 2,000–2,800 (3,300) m elevation. (undesignated)

*Arenaria quirosii* Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 22:19. 1940.

Small herbs, the stems to 6 cm tall, erect; internodes 1.5–5 mm long, densely pubescent with multicellular trichomes to 0.3 mm long. Leaves opposite, sessile, the laminae 2.5–5 mm long, 1–2.5 mm broad, ovate to obovate, apically acute to obtuse and short-acuminate with the tip often thickened and brownish (dry), the base broadly attenuate, the margin entire, the lamina drying thick-chartaceous and yellowish to brownish, sparsely puberulent above and below, sparsely to densely ciliate along the midrib below and along the proximal  $\frac{2}{3}$  of the margin, only the midvein conspicuous. Flowers solitary and axillary, the pedicels 2–4 mm long, densely pubescent with short multicellular hairs; sepals 5, 2.2–3 mm long (anthesis to fruiting), lanceolate to oblong-ovate, the apex short-acuminate, the tip often thickened and brownish, margins rather broad and scarious, ciliate along the midvein; petals absent; stamens 10, the filaments 0.5–0.8 mm long, anthers 0.2 mm long (anthesis); ovary ovoid, ca. 0.6 mm long (anthesis); styles 3, ca. 0.4 mm long (anthesis) to 1.2 mm long (fruit). Fruit a capsule, ellipsoid, the valves after dehiscence approximately equaling the sepals (ca. 3 mm); seeds numerous, 0.7 mm broad, reniform-globose, seed coat smooth and shiny, dark maroon to black.

*Arenaria quirosii* can be recognized by its very small habit, its small broad leaves, its short pedicels, and its lack of petals. This species was known only from the type collection (*M. Quiros* C. 812 collected on Volcan Irazu in September 1938), but has recently been found on Costa Rica's highest mountain, Chirripó, by Arthur Weston.

## CERASTIUM Linnaeus

*By David Good*

Herbs, annual or perennial, low and caespitose to tall and erect, often ascending, stems almost always puberulent, with or without glandular hairs; stipules absent. Leaves opposite and sessile or subsessile, a basal rosette present or absent, cauline leaves few to many, usually shorter than the basal leaves when the latter are present; laminae linear to elliptic, ovate or spatulate, acute or obtuse at the apex, often clasping the stem at their base and the opposing leaf bases sometimes united, entire, usually puberulent. Inflorescence invariably a cyme, either compact or loose, borne on distal stems, usually puberulent. Flowers very small (2–3 mm) to medium sized (ca. 1 cm), bisexual, radially symmetrical, sepals 5 (4), free, lanceolate to elliptic, acute, scarious margined, usually pubescent, petals 5 (4, 0), free, usually white, variously bifid; stamens 10 (5, 4), free, shorter than the petals; ovary superior, carpels and styles 5 (rarely 4 or 3), opposite the sepals. Fruit a capsule, usually well exserted beyond the persisting sepals at maturity and opening apically by twice as many teeth as there were styles; 1-locular, thin walled, often curved at maturity; seeds many, small (0.3–1.2 mm), cochleate to U-shaped or subcircular in outline, somewhat compressed, the surface variously tuberculate.

A virtually cosmopolitan genus of 50 to 100 species of small more or less scruffy herbs. These plants are confined to cooler habitats and are not found below 1,200 m elevation in Central America. The genus can be confused with any of several other genera in the Caryophyllaceae, particularly with *Stellaria* and *Arenaria*, but the presence of five styles, considerable pubescence, and the exserted curved capsules usually set it apart. Flowers of Costa Rican species are all five-parted, with five sepals, five petals, 10 stamens, and five styles.

- 1a Cauline leaves elliptic to ovate or obovate, usually obtuse to rounded at the apex; pedicels 1–5 mm long, sepals 2.5–5 mm long; capsules 5–8 mm long, seeds 0.3–0.4 mm in diameter. . . . . *C. glomeratum*



- 1b Cauline leaves linear to lanceolate or narrowly elliptic, acute to acuminate at the apex; sepals 4.3–6.5 mm long; capsules 7–12 mm long ..... 2a
- 2a Pedicels up to 14–35 mm long; petals divided for  $\frac{1}{8}$  of their length; seeds 0.8–1 mm in diameter ..... *C. guatemalensis*
- 2b Pedicels 2–9 mm long; petals divided for  $\frac{1}{3}$  of their length; seeds 0.5–0.7 mm in diameter ..... *C. triviale*

***Cerastium glomeratum*** Thuillier, Fl. Paris, ed. 2, 226. 1799. *C. viscosum* L. (nom. ambig.), Sp. Pl. 437. 1753.

Annual plants with stems ascending or erect, sometimes caespitose, 2.5–30 cm tall, very much branched at the base, little otherwise, branches pilose, leafy internodes usually longer distally than basally, longer or shorter than the leaves. Leaves  $\pm$  similar throughout, perhaps slightly smaller above, basal rosette lacking; laminae broadly elliptic to orbicular or spatulate, 5–20 mm long, 3–12 mm wide, obtuse, pilose. Basal rosette lacking. Cymes many flowered, flowers very crowded terminally, pedicels very short, 1–5 mm long, pilose, sometimes slightly glandular. Sepals lanceolate, 2.8–5.1 mm long, 0.5–1.6 mm wide, acute, scarious margined, pilose, sometimes glandular; petals shorter than or equal to the sepals, bifid ca.  $\frac{1}{4}$  of their length, white; filaments 1.8–2.3 mm long, anthers 0.1 mm long; styles 0.8–1.1 mm long. Capsules 5.0–8.8 mm long, 1.3–1.8 mm wide, curved; seeds 0.3–0.4 mm in diameter, finely tuberculate.

An introduced species of varied habitats including roadsides, fields, woodlands, volcanic rocks, cornfields, gardens, and other areas. In Costa Rica it has been collected at altitudes of between 1,460 and 2,600 m in the provinces of Alajuela, Cartago, and San Jose. Native to Europe, *Cerastium glomeratum* is found in North America throughout much of the southern and central United States, in central Mexico, and from southern Mexico (Chiapas) south to Chiriqui Province, Panama. Flowering specimens can be found virtually throughout the year.

*Cerastium glomeratum* is recognized by its usually broadly elliptic-ovate leaves, its bracts lacking scarious margins, and its inflorescences of very small, very crowded flowers.

***Cerastium guatemalense*** Standley, Field Mus. Nat. Hist., Bot. Ser. 17:244. 1937. Figure 42.

Perennial plants with stems to 45 cm tall, often much branched basally and above, branches erect or ascending, densely glandular-pilose, internodes usually more or less equal except at the base, where shorter. Leaves usually similar throughout or the lower ones somewhat shorter, basal rosette lacking; laminae linear to lanceolate, widest at the base, narrowing to an attenuate tip, 15–48 mm long, 2–5 mm wide, glandular-pilose, particularly on the lower surface. Cymes 3–40 flowered, usually 3–15, bracts not scarious margined, lowermost (longest) pedicels 14–35 mm long, upper ones shorter, all  $\pm$  hooked in fruit, glandular-pilose. Sepals lanceolate, 4.4–6 mm long, 1–1.7 mm wide, acute, scarious margined except at the apex, glandular, petals 6–7.1 mm long, bifid ca.  $\frac{1}{8}$  of their length, white; filaments 3.2–3.5 mm long, anthers 0.3 mm long; styles 1.9–2.1 mm long. Capsules 7.8–11.8 mm long, 2–2.8 mm wide, curved; seeds tuberculate, 0.8–1 mm in diameter.

Species of the high (2,100 to 4,400 m) pine and juniper forests on many of the volcanoes of Guatemala and adjacent Mexico. It is also sometimes found in open upland meadows. In Costa Rica, only a single collection has been made (*Burger and Gomez P. 8216*), and it probably represents a disjunct population. This collection was made at 3,250 to 3,450 m altitude on Cerro Chirripo along the upper Rio Talari, Prov. San Jose. In the main part of its range, this species has been collected in flowering condition in January, February, and July through October. It probably flowers to some degree throughout the year.

*Cerastium guatemalense* is distinguished by its more or less erect habit and its open inflorescences of relatively (compared to *C. triviale* and particularly to *C. glomeratum*) large flowers. It is the only native species of *Cerastium* ever collected in Costa Rica.

***Cerastium triviale*** Link, Enum. Hort. Berol. 1:433. 1821. *C. vulgatum* L. (nom. ambig.), Sp. Pl., ed. 2, 627. 1762. *C. caespitosum* Gilibert (nom. ambig.), Fl. Lithuan. 2:159. 1781. *C. holosteoides* Fries (nom. ambig.), Novit., ed. 2, 126. 1823. *C. fontanum* subsp. *triviale* (Link) Jalas, Arch. Soc. Zool. Bot. Fenn. "Vanamo" 18:63. 1963.

Weakly perennial plants, much branched, mostly basally, often caespitose, branches 10–25 cm long, decumbent, often long-pilose, internodes longest just below the inflorescence, shorter below. Leaves usually similar throughout, basal rosette lacking; laminae ovate to spatulate, 7–30 mm long, 3–10 mm wide, acute, sometimes obtuse, pilose. Cymes usually quite dense, few to many flowered, bracts with scarious margins, pedicels short, 2.2–8.4 mm long, long-pilose. Sepals lanceolate, 4.3–6.2 mm long, 1–1.6 mm wide, scarious margined, acute, pilose, petals slightly shorter to slightly longer than the sepals, bifid ca.  $\frac{1}{3}$  of their length, white; filaments 3.7–4 mm long, anthers 0.3 mm long; styles 1.8–2.2 mm long. Capsules 7–11.6 mm long, 2.1–3 mm wide, curved; seeds 0.5–0.7 mm in diameter, red-brown, tuberculate.

An introduced upland species (in our area 1,400 to 2,400 m) of varied habitats including fields, roadsides, brushy thickets, woody areas, and even cloud forest. Native to Europe, this species is found in North America throughout most of the United States and southern Canada, in central Mexico and in Central America from southern Mexico (Chiapas) south to Chiriqui Province, Panama. In Costa Rica it has been collected virtually throughout the year from the provinces of Alajuela, Cartago, and San Jose.

*Cerastium triviale* is recognized by its prostrate habit, its fairly broad leaves, its scarious margined bracts, and its inflorescences of crowded, fairly small (though larger than in *C. glomeratum*) flowers. The choice to use the name *C. triviale* in this work instead of *C. fontanum* subsp. *triviale* is arbitrary. Sound judgment on the best taxonomic level for this taxon would require study of European material.

### DIANTHUS Linnaeus

Herbs, biennial or perennial, stems often stiff and erect, nodes usually thickened, glabrous or glaucous (rarely puberulent); stipules absent. Leaves opposite and narrow, sessile, leaf bases of opposing leaves connate and forming a short scarious sheath, laminae entire or serrulate. Inflorescences terminal and often showy, capitate, cymose or paniculate or the flowers solitary, flowers subtended by 1–3 opposing pairs of bracts. Flowers radially symmetrical, bisexual, sepals united to form a calyx tube, 5-toothed at the apex of the tube, with multiple parallel veins; petals 5 or more, usually narrowed at the base to form a petiole-like structure (clawed), the distal blade of the petal entire to dentate or fringed, lacking appendages at the base, white to rose, red or purple; stamens 10, free; ovary superior and unilocular, narrowed at the base or stipitate, styles 2, free. Fruit a capsule, cylindric to oblong or ovoid, dehiscent by 4 (5) valves or teeth; seeds numerous, usually flattened and with an oval outline, attached on 1 of the flat faces, smooth to rugose.

A genus of between 200 and 300 species native to the Old World. The four species mentioned here are the most showy and popular of the species that may be found in cultivation in the tropics. Each of these four species represents one of a total of nine horticultural classes listed in Bailey's Manual of Cultivated Plants. Bailey's manual lists more than 30 species and varieties grown in gardens

throughout the world; they generally grow best only at higher elevations in the tropics. This genus is distinguished from our other ornamental genera by the presence of one to three pairs of appressed bracts at the base of the calyx tube.

- 1a Flowers crowded into dense round-topped or flat-topped heads, bracts linear and usually as long as the calyx (sepal tube) ..... *D. barbatus*
- 1b Flowers in loose cymes with 2 to many flowers (note that individual flowers with multiple petals in *D. caryophyllus* may appear similar to heads, but each one is enclosed in a single calyx tube), bracts shorter than the calyx tube ..... 2a
- 2a Bracts  $\frac{1}{2}$ – $\frac{2}{3}$  the length of the calyx, caudate at the apex; leaves narrow-elliptic to oblanceolate ..... *D. chinensis*
- 2b Bracts  $\frac{1}{4}$ – $\frac{1}{3}$  the length of the calyx, acuminate at the apex; leaves linear ..... 3a
- 3a Leaf margins and bract margins minutely serrulate to subentire or ciliate, leaves mostly in a basal tuft and with few stem leaves; flowers not double (with 5 petals) ..... *D. plumarius*
- 3b Leaf margins and bract margins entire and glabrous, with prominent stem leaves; flowers usually double (10 or more petals); an important species in cut-flower commerce ..... *D. caryophyllus*

***Dianthus barbatus* L., Sp. Pl. 409. 1753.**

Perennial herbs, glabrous, stems erect, 20–60 cm tall. Leaves with lanceolate to elliptic laminae, 3.5–8 cm long, 0.5–1.5 cm wide, apically acute, the margins usually minutely (0.1–0.5 mm) serrulate (appearing almost ciliate). Inflorescence a dense terminal cyme that often appears capitate, floral bracts linear to filiform, usually equalling the calyx in length; flowers numerous within the cyme and sessile, calyx deeply toothed, the teeth long-acuminate, distal lamina of the petals dentate or crenate, red, purple, pink, white or variegated, corolla not usually more than 3 cm broad, rarely double.

*Dianthus barbatus* is a native of southern Europe and is representative of the horticultural group called "Sweet Williams" and *Clavel Imperial*. They are characterized by having small flowers in bracteate heads. As with the other species mentioned here, many variants and hybrids with other species are found in cultivation.

***Dianthus caryophyllus* L., Sp. Pl. 410. 1753.**

Glabrous and glaucous herbs, the stems erect and stiff, few branched, with conspicuous nodes, to 1 m tall. Basal leaves 5–15 cm long, linear and stiff, the margins entire or minutely serrulate near the base, leaves of the stem becoming smaller distally. Inflorescence cymose, few flowered, floral bracts ca.  $\frac{1}{4}$  as long as the calyx, abruptly acute, pedicels subtending the flowers and their involucre of bracts to 3 cm long; calyx 2–3 cm long, calyx teeth acute, petals usually double (10), rose, purple, or white, corolla 2–9 cm broad and showy, very fragrant.

*Dianthus caryophyllus* is native to southern Europe. The "Carnation" (*Clavel*) is perhaps the most popular of all the species of *Dianthus*, cultivated for its showy and fragrant flowers. The distinctive odor is similar to cloves (*Clavero*; *Syzygium aromaticum*) and cinnamon (*Canela*; *Cinnamomum zeylanicum*). In Costa Rica it is cultivated at the middle and higher altitudes, and it is a very important element in the ornamental cut-flower trade (see discussion in the Flora of Guatemala, Fieldiana, Bot. 24, pt. 4:226–227, 1946).

***Dianthus chinensis* L., Sp. Pl. 411. 1753.**

Herbs, short-lived perennials, glabrous or nearly so, the stems erect. Basal leaves caducous, stem leaves 2–8 cm long, 0.5–1 cm wide, narrowly elliptic to oblanceolate, acute at

the apex, usually minutely serrulate along the margins. Inflorescence cymose, few to many flowered, pedicels to 2 cm long, floral bracts ca.  $\frac{1}{2}$  as long as the calyx or slightly longer, cuspidate to caudate at the apex, often divergent; calyx 1.5–2.5 cm long, calyx teeth acute to acuminate, petals rarely double, variously colored, the corolla often with concentric or circular patterns, to 3 cm broad, odorless.

*Dianthus chinensis* is a native of eastern Asia. The circular patterns of the broadly rotate corolla have resulted in the common name "Rainbow Pinks" for these plants. Because of the smaller flowers they have been called *Clavellina* in Spanish.

***Dianthus plumarius* L., Sp. Pl. 411. 1753.**

Glabrous or glaucous herbs, the stems caespitose, to 30 cm long. Basal leaves 2–10 cm long, linear, the margins minutely serrulate, stem leaves becoming smaller distally. Inflorescence cymose and few flowered, the pedicels to 4 cm long, floral bracts  $\frac{1}{4}$ – $\frac{1}{3}$  the length of the calyx, relatively broad, acute to acuminate at the apex; calyx ca. 2 cm long, the teeth acute, petals dentate or more commonly deeply fringed, red, pink or white, the corolla 3–4 cm broad, fragrant.

*Dianthus plumarius* is native to eastern Europe and Russia. It is representative of a group called the "Cottage Pinks," characterized by their fragrant flowers and tufted habit.

**DRYMARIA Willdenow**

REFERENCE: James A. Duke, Preliminary Revision of the Genus *Drymaria*, Ann. Missouri Bot. Gard. 48:173–268, 1961.

Herbs, annual or perennial, stems procumbent to erect, occasionally slightly woody at the base, glabrous or puberulent; stipules present, entire to multilacerate, caducous or persistent. Leaves opposite (in ours) or appearing verticillate, sessile or petiolate; laminae broad and flat (in ours) to linear, margin entire or rarely dentate, venation palmate to parallel. Inflorescences dichasial (in ours), terminal or axillary or with flowers clustered or solitary at the nodes; flowers bisexual, radially symmetrical, small, sepals 5, free, green with scarious or membranous margins, lanceolate to ovate, petals 3, 4 or 5 (rarely 0), normally 2-cleft (bifid) at the apex or distal half and often with small auricles at the base; stamens 2–5, filaments slightly connate at the base (rarely alternating with staminodes), the anthers versatile, 2-thecous; ovary superior and narrowed at the base, unilocular, placentation free central with few to many ovules, styles usually 3 (2) and united for ca.  $\frac{1}{2}$  their length. Fruit a capsule, ovoid to globose, dehiscent by as many valves as there are styles (usually 3-valved), thin-walled; seeds 1 to many, cochleate (in ours) to reniform-globose, usually with the surfaces and edges tuberculate, embryo curved.

A genus of 48 species, according to Duke, ranging from the southern United States to subtropical South America and with two of these species now naturalized in Asia and Africa, Australia, and the Pacific. Three species occur in Costa Rica in areas characterized by evergreen (or largely evergreen) vegetation and the genus can be found at all elevations.

Vegetatively, the Costa Rican species of *Drymaria* resemble those of *Stellaria*, and the two are occasionally confused. *Drymaria* differs from *Stellaria* by having three-valved capsules, partly united styles, and by the presence of stipules. However, the stipules are often caducous or difficult to distinguish from the surrounding trichomes and this feature may not be helpful. Species of *Stellaria* with broad leaves are pinnately veined with a more or less distinct submarginal collective vein. In contrast, *Drymaria* has one to five parallel or palmate primary veins and lacks a submarginal collective vein.



- 1a Flower pedicels covered in part with a minute dense gland-tipped tomentum that is whitish, petals often smaller than the sepals; stipules multilacerate and usually persistent; common plants from 0–1,600 m elevation ..... *D. cordata*
- 1b Flower pedicels glabrous to sparsely hirsute or villous or glandular, never with a minute dense whitish or farinose tomentum; petals usually as large or larger than the sepals; uncommon or rare plants ..... 2a
- 2a Plants hirsute to glabrate; laminae rarely more than 10 mm broad, drying opaque and the venation obscure; stipules lacerate with filiform hairlike lobes but caducous; sepals 2–3.5 mm long, elliptic to ovate; plants usually found from 1,000–2,000 m elevation ..... *D. villosa*
- 2b Plants glabrous to sparsely glandular hairy; laminae usually more than 10 mm broad, drying membranaceous and the venation easily seen; stipules with lanceolate lobes and persistent; sepals 3–6 mm long, 1,600–3,000 m elevation. .... *D. multiflora*

***Drymaria cordata* (L.) Willd. ex Roem. & Schult., Syst. Veg. 5:406. 1819.**  
*Holostium cordatum* L., Sp. Pl. 88. 1753. *H. diandrum* Sw., Prodr. 27. 1788. *D. diandra* Blume, Fl. Nederl. Ind. 62. 1825. Figure 42.

Herbs, annual, prostrate to spreading or erect, to 70 cm long, often rooting at the nodes, glandular puberulent to glabrate, leafy internodes 0.5–3 cm long, ca. 0.5 mm thick (dry); stipules to 2 mm long, lacerate, often persisting. Leaves opposite and usually well spaced along the stem, petioles 2–15 mm long; laminae 5–18 (25) mm long, 5–20 (30) mm broad, broadly ovate to orbicular or reniform, rounded at the apex and occasionally mucronulate, abruptly rounded at the base and truncate to cordate, entire, usually glabrous. Inflorescences terminal or axillary, few- to many-flowered cymes (rarely solitary axillary flowers), bracts 2–3 mm long, narrowly lanceolate, pedicels 2–15 mm long, slender and usually with a covering (at least in part) of very minute (0.1 mm) whitish glandular puberulence. Flowers small; sepals 5, 2.5–4 (5) mm long, lanceolate to ovate, acute, glandular puberulent to glabrous, lateral margins translucent, petals 5, 2–3 mm long, deeply bifid with linear 1-veined lobes, lacking auriculae (rarely subdentate) at the base; stamens 2 or 3 (4, 5), filaments 2–2.5 mm long and flattened, anthers suborbicular, 0.2–0.3 mm long; ovary with few to many ovules, style 0.5–1 mm long, 2- or 3-parted. Capsule ovoid, 1.5–2.5 mm long, breaking into 3 entire valves; seeds 1 to many, 1–1.5 mm broad, cochleate, dark reddish brown, surface with rows of tubercles.

Plants of open sunny or shaded (early secondary) sites in areas of evergreen vegetation in the Central Highlands and Caribbean side of Costa Rica from near sea level to 1,400 (1,600) m elevation; collected with flowers throughout the year in southern Central America. Our plants belong to subspecies *cordata* which ranges throughout the American tropics, from Mexico and Florida through Central America and the West Indies to Argentina. Subspecies *diandra* (Blume) Duke occurs in tropical Asia, Africa, Australia, and the Pacific.

*Drymaria cordata* is recognized by the small opposite, often broadly cordate, leaves that are usually evenly spaced along the slender stems, the unusual puberulence producing a farinose-like whitish covering on a portion of the flower pedicels and the small petals. This species has not been collected from below 1,000 m elevation on the Pacific side of Costa Rica.

***Drymaria multiflora* Brandegees, Zoe 5:232. 1906.**

Herbs, perennial, erect or ascending, to 50 cm tall, much branched (in vigorous plants), glabrous to stipitate-glandular (rarely sparsely villous), leafy internodes 1–10 cm long, 0.5–1.5 mm thick (dry); stipules 1–2.5 mm long, lanceolate, entire. Leaves opposite and often widely spaced, petioles 2–20 mm long; laminae 4–22 mm long, 4–25 mm broad, broadly deltoid-ovate to orbicular or reniform, rounded to emarginate at the apex, obtuse to truncate at the base, entire, drying membranaceous, the 3–5 primary veins often clearly visible. Inflorescences terminal, cymose with 3 to many flowers, peduncles to 10 cm long, often stipitate-glandular. Flowers small, whitish, sepals 5, 3–6 mm long, 1.2–2 mm broad,

ovate to narrowly triangular, often saccate at the base, petals 5, 2.5–7 mm long, equalling or exceeding the sepals, bifid for  $\frac{2}{3}$  of their length, lobes rounded, with ciliate auricles at the base; stamens 3–5, 2–3.5 mm long, anthers 0.3–0.5 mm long; ovary globose to ovoid, styles 1–2 mm long, 2- or 3-parted. Capsule 2–3.5 mm long, ovate, with 4–26 seeds; seeds ca. 1 mm broad, with long dorsal tubercles and substellate facial tubercles.

Rare plants (in Costa Rica) of shaded sites in montane forest between 1,500 and 3,000 m elevation. Flowering collections have been made from October to February in Central America. The species ranges from Mexico to westernmost Panama.

*Drymaria villosa* Cham. & Schlecht., *Linnaea* 5:232. 1830. *D. hirsuta* Bartl. in Presl, *Rel. Haenk.* 2:8. 1831.

Herbs, annual, prostrate or more often ascending, to 45 cm long, sparsely villous to hirsute with slender translucent hairs to 2 mm long, leafy internodes 0.5–5 cm long, ca. 0.5 mm thick; stipules 0.5–1.5 mm long, slender and usually entire, similar to the trichomes. Leaves opposite and usually evenly spaced along the stems, petioles 1–10 mm long; laminae 3–15 mm long, 3–15 mm broad, orbicular to reniform or broadly ovate, rounded to acute at the apex, rounded at the truncate to subcordate base, entire, usually sparsely hirsute or villous. Inflorescences cymose, terminal or axillary, with 5 to many flowers (ultimate parts often racemose), peduncles 1–5 cm long, bracts 0.5–1.5 mm long, pedicels 2–20 mm long, slender and sparsely villous. Flowers whitish, sepals 5, 2–3.6 mm long, 1–2 mm broad, elliptic to broadly ovate, acute to obtuse at the apex, villous to glabrescent, margins translucent, petals 5 (rarely reduced or absent), 2–3.6 mm long, divided distally into 2 parts (bifid) for half their length or more, 4-veined, with caducous filiform auricles at the base, stamens usually 5, 2–3.5 mm long; ovary ovoid to globose, style 1–1.5 mm long, the distal half 3-parted. Fruit an ovoid to ellipsoid capsule, 2–3.5 mm long, equalling or exceeding the sepals; seeds usually many, 0.5–0.9 mm broad, cochleate, tuberculate with the facial tubercles stellate.

Small weedy plants of open sunny sites in evergreen vegetation formations, primarily between 1,000 and 2,000 m elevation, in Costa Rica. Flowering and fruiting collections have been made from June through the wet season to March. This species is represented in our area by *ssp. villosa*; this subspecies ranges from Mexico through Central America and along the western slopes of South America to Peru.

*Drymaria villosa* *ssp. villosa* is characterized by its small stature, its open dif-fused branches and inflorescences, pubescence of slender translucent hairs, the small broad subcordate opposite leaves well spaced along the stem, and the slender peduncles and pedicels bearing small 5-parted flowers.

### GYPSOPHILA Linnaeus

Herbs or rarely shrubs, annual or perennial, erect or spreading, usually much branched, glabrous or glaucous; stipules absent. Leaves opposite, often narrow and sessile or subsessile, entire. Inflorescences cymose in dichasial or paniculate arrangements (rarely capitate), with numerous flowers, bracts present at the base of pedicels and not at the apex (an epicalyx lacking). Flowers small, bisexual, radially symmetrical, calyx forming a tube or united only near the base and campanulate, 5-toothed and 5-veined, scarious (thin) between the veins, petals 5, exceeding the sepals, white to rose, usually narrowed at the base (with a claw) and the expanded blade entire to emarginate, lacking appendages near the juncture of claw and blade; stamens 10; ovary 1-locular and with many ovules, styles 2 (3), free. Fruit a capsule, ovoid to globose, dehiscing by 4 (6) valves or teeth, sessile; seeds with flattened faces, subreniform, black and tuberculate.

A genus of about 125 species native to Europe and Asia, with outlying species in Egypt and Australia. One species is commonly cultivated in Central America,

while a second species (*G. paniculata* L.), growing to 1 m tall and with a stout rhizome, may also be found. Both are called "Baby's Breath," *Gipsophila*, or *Llovisna*. The open panicle of small long-pedicelled flowers give a diffuse misty effect, both in gardens and in flower arrangements. The inflorescences are sometimes sprayed with paint for more colorful effects.

***Gypsophila elegans* Bieb., Fl. Taur. Cauc. 1:319. 1801.**

Annual herbs, stems erect, to 60 cm tall, much branched distally, glabrous. Leaves sessile, 2–7 cm long, 0.2–1 cm broad, linear-lanceolate to lanceolate, leaf bases clasping the stem and the opposing leaf bases slightly connate or free. Inflorescences cymose, open and much branched and with many flowers, pedicels 1–3 cm long, slender or filiform. Flowers small, calyx 4–5 mm long, calyx tube half the length and campanulate, weakly 5-veined, calyx lobes acute and with thin margins, petals 2–4 × the length of the calyx, white to red, emarginate; stamens 4–5 mm long; ovary ca. 2 mm long, ovoid, styles ca. 3 mm long, filiform. Capsule 3.5–5 mm long, ovoid; seeds 1–1.5 mm broad, tuberculate.

*Gypsophila elegans*, a native of the Caucasus mountain region, Turkey and Iran, is locally naturalized in Guatemala and commonly grown in gradens. This species is important in the cut-flower trade for its many-branched diffuse inflorescences for which the name *Llovisna* is so appropriate.

**LYCHNIS Linnaeus**

Herbs, annual or perennial, stems erect; lacking stipules. Leaves opposite. Inflorescences cymose, often lax and few flowered or capitate and many flowered. Flowers usually bisexual, radially symmetrical, without an epicalyx, calyx united to form an ovoid to obovoid tube, 10-veined, petals 5, with a proximal narrow claw and distal blade, entire to bifid, emarginate or lacerate at the apex, usually with adaxial appendages at the junction of claw and blade; stamens 10, filaments united only at the base; pistil short-stipitate, ovary incompletely 5-locular at the base and 1-locular near the apex, with many ovules, styles usually 5, free. Fruit a capsule dehiscent by 5 teeth (less often 10), borne on a short stalk; seeds circular to reniform, surface minutely tuberculate.

A genus of about 35 species of north temperate and arctic areas. One species is likely to be found at higher elevations in tropical American gardens.

***Lychnis coronaria* (L.) Desr., Lam. Encyc. 3:643. 1792. *Agrostema coronaria* L., Sp. Pl. 436. 1753.**

Herbs perennial, erect to 1 m tall, all parts densely white-tomentose (woolly). Basal leaves spatulate and petiolate, 5–18 cm long, stem leaves sessile and smaller, narrowly ovate to elliptic, acute at the apex, clasping the stem at the base. Inflorescence a compound dichasium of only a few flowers, pedicels 4–10 cm long, thick and white-woolly. Flowers showy, calyx 15–20 mm long (including the calyx teeth), teeth contorted in bud, ca. 5 mm long, linear, petals ca. 3 cm long, the blade usually equaling the claw, appendages 2.5–3 mm long present at the junction of claw and blade; stamens ca. 14 mm long; styles 5, ca. 3 mm long, free. Capsule ca. 12 mm long, borne on a stipe ca. 2 mm long, teeth spreading at the apex of the capsule; seeds numerous, less than 1 mm broad.

*Lychnis coronaria*, the "Rose Campion" or *Españolita*, is easily recognized by its densely white-woolly stems and leaves and its large deep rose- or purple-colored flowers. This species is native to southeastern Europe and generally found only in gardens above 1,800 m elevation in Central and South America.

**POLYCARPON Loefling ex Linnaeus**

Herbs, annual or perennial, stems diffuse or dichotomously branching, usually less than 30 cm long, internodes with minute longitudinal ridges, glabrous or puberulent; stipules

present and scarious. Leaves opposite or whorled, laminae obovate to orbicular, entire. Inflorescences cymose, with few or many branches, flowers subtended by scarious bracts and usually pedicellate. Flowers small, bisexual, radially symmetrical, sepals 5, with keeled or prominent midrib and thin margins, free, petals 5, hyaline and smaller than the sepals, free; stamens 1–5, filaments united at the base; ovary unilocular, ovules few to many on a free central placenta, style short and 3-lobed. Fruit a 3-valved capsule, valves splitting almost to the base, becoming spirally twisted; seed ovoid to lenticular or curved, embryo incurved or almost straight.

A cosmopolitan genus of temperate regions and cooler tropical highlands, with about 15 species. A number of species are known from southern South America, but the genus has not been previously recorded from Central America.

**Polycarpon tetraphyllum** (L.) L., Syst. Nat. ed. 10, 2:881. 1759. *Mollugo tetraphylla* L., Sp. Pl. 1:89. 1753.

Small herbs, annual or rarely perennial (lacking a woody rootstock), stems often much branched, to 20 cm long, essentially glabrous, internodes 5–15 mm long, with thin and minutely serrulate ridges; stipules conspicuous, 2–3 mm long, triangular, thin and translucent, erose to cuspidate with a long slender tip. Leaves opposite or in whorls of 4, petioles ca. 3 mm long; laminae 0.3–1 cm long, 2–6 mm broad, narrowly obovate to oblong-obovate, bluntly rounded at the apex, tapering gradually to the attenuate base, essentially glabrous, secondary venation obscure. Inflorescence with few or many branches, cymose, floral bracts whitish translucent, 1–2 mm long and resembling the stipules. Flowers small, 2–3 mm long, sepals 1.5–2 mm long, dark green along the midvein and somewhat keeled, margins thin and translucent, petals smaller than the sepals, emarginate; stamens usually 3–5. Fruit less than 3 mm long; seeds ca. 0.5 mm long, semicircular or slightly lunate in outline, pale orange-brown.

Weedy little plants from Europe often found on sandy or rocky soil. The first collection recorded for Central America was made in June 1982 on the slope of Volcan Irazu near Tierra Blanca, Cartago, at an elevation of 2,100 m by Jorge Gomez-Laurito (8630). The species is naturalized in South America and in Mexico.

*Polycarpon tetraphyllum* is recognized by its very small stature, the two or four small obovate leaves at each node, the conspicuous stipules, the cymose inflorescences, and the small flowers with slightly "keeled" sepals.

#### SAGINA Linnaeus

REFERENCE: Garrett E. Crow, A Taxonomic Revision of *Sagina* (Caryophyllaceae) in North America, *Rhodora* 80:1–91, 1978.

Herbs, annual or perennial, stems procumbent, decumbent or ascending, sometimes slightly woody at the base, short in stature, stems glabrous or glandular puberulent; stipules absent. Leaves opposite along the stem, rosettes or tufts of basal leaves may be present in perennial species, without distinct petioles; laminae of the cauline leaves linear to subulate, simple and entire, clasping the stem at their base and connate with the opposing leaf base. Inflorescences of solitary flowers, terminal or in the axils of distal leaves; flowers bisexual, radially symmetrical, small, whitish; ebracteate; sepals 4 or 5, free, obtuse and with scarious margins, imbricate, petals 4 or 5 (rarely fewer or none), free, entire or slightly emarginate; stamens 4, 5, 8 or 10, equalling or twice as many as the styles, in 1 or 2 whorls, nectaries present at the base of the outer whorl, filaments free, anthers dehiscing longitudinally and extrorse; ovary superior and unilocular, placentation free central with numerous ovules, styles the same number as the sepals and alternate with them, united at the base, becoming recurved. Fruit a many-seeded capsule breaking into 4 or 5 valves, the valves opposite the sepals and thin-walled; seeds usually 0.3–0.5 mm broad, reniform to triangular or subglobose, surface smooth to papillate or tuberculate.



A genus of 15 species, chiefly of the cold temperate zone of the Northern Hemisphere; centers of diversity are Europe and eastern Asia. Our species is a Eurasian introduction which has become established at higher elevations in Mexico, Guatemala, and Costa Rica.

***Sagina procumbens* L., Sp. Pl. 128. 1753. Figure 41.**

Herbs, perennial, usually procumbent and very small (less than 10 cm tall), much branched from the base, stems to 15 cm long, glabrous throughout. Leaves of the stems opposite and sessile, basal leaves 4–15 mm long, distal leaves 2.5–7 mm long, less than 1 mm broad (dry), linear and entire, apiculate to aristate at the tip, united at the base to form a short (0.5 mm) scarious sheath. Flowers borne on slender pedicels (3) 5–10 (13) mm long, perianth usually 4-parted, sepals 4 (5), elliptic to orbicular, 1.5–2.5 mm long, ca. 1 mm wide, margins white, petals usually 4, 0.7–1.4 mm long, often half as long as the sepals, orbicular to obovate or elliptic; stamens 4 (8), filaments 1–1.5 mm long, anthers 0.3 mm long; ovary 1–2 mm long, styles ca. 0.6 mm long. Fruit 2–3 mm long, enclosed by the persisting sepals which open out as the capsule dehisces; seeds brown, reniform to obliquely triangular, with a distinct dorsal groove, ca. 0.4 mm broad, smooth.

A weedy species of open, often gravelly or sandy, sites, flowering throughout the year in Central America at altitudes from 1,100 to 3,700 m elevation. This species is a native of Eurasia and has only been found around the eastern edge of the Meseta Central in Costa Rica and along the Interamerican Highway.

*Sagina procumbens* is recognized by its very small habit and its little linear opposite leaves forming a sheath at their base, the solitary pedicellate flowers with sepals larger than the petals and the small capsular fruit with minute somewhat triangular seeds.

**SAPONARIA Linnaeus**

Herbs, annual or perennial, the stems erect or spreading; stipules absent. Leaves opposite, simple and entire. Inflorescence cymose, loosely flowered to capitate. Flowers bisexual, radially symmetrical, lacking an epicalyx, calyx united to form a tube with 5 teeth at the apex, many veined but the veins often obscure, petals 5, longer than the calyx, the base narrowed into a claw, the expanded distal blade of the petal entire or emarginate, appendages usually present on the base of the blade above the claw (adaxial surface); stamens 10, united at the base to form a short tube around the stipe; pistil borne on a short stipe, ovary 1-locular, many ovulate on a free-central placenta, styles usually 2 (3), free. Fruit a capsule opening only at the apex with 4 (6) short teeth, ovoid to oblong, smooth; seeds reniform and tuberculate.

A genus of about 30 species of Europe and adjacent Asia, but most numerous in the Mediterranean area. The following species is occasionally cultivated in the highland tropics and is widely naturalized in north temperate North America.

***Saponaria officinalis* L., Sp. Pl. 408. 1753.**

Perennial herbs, stems erect and stout but little branched, glabrous, nodes thickened and with an interpetiolar line formed by the connate opposing leaf bases. Leaves sessile or subsessile, laminae 5–9 cm long, 1–2.5 cm wide, ovate lanceolate to elliptic, acute at the apex, attenuate at the base and clasping the stem, entire, with 3 distinct primary veins impressed above. Inflorescences of opposing few-flowered dichasia clustered toward the ends of the branches, pedicels 1–3 mm long, their subtending bracts often leaflike. Flowers showy, calyx 15–25 mm long, tubular, calyx teeth ca. 5 mm long and with a mucronate (1 mm) tip, petal claw 20–27 mm long, petal blade 10–15 mm long, emarginate and white to pale rose, 2 linear appendages ca. 1 mm long at the base of the blade above the claw; stamens 10, exceeding the petal claws in length; ovary to 15 mm long and 2 mm thick, styles 2, ca. 15 mm long, filiform. Capsule narrowly ovoid to ellipsoid, to 20 mm long and

8 mm thick, dehiscing by 4 teeth ca. 0.5 mm long and becoming recurved, the calyx tube persistent and enclosing the fruit; seeds to 2 mm broad, reniform, surface with concentric rows of tubercles.

*Saponaria officinalis* is a native of Europe and may be found in gardens at higher elevations in Central America. Both the Latin name and the English name "Soapwort" are derived from the fact that the leaves give a lather when rubbed with water.

### SCLERANTHUS Linnaeus

Herbs, annual, biennial or perennial, procumbent to erect, usually densely branched, glabrous or minutely puberulent; stipules absent. Leaves opposite, clasping the stem at their base and with the opposing leaf bases often united to form a short sheath, laminae entire and narrow, small. Inflorescences dense terminal or axillary cymose clusters (in ours) or solitary flowers in leaf axils; flowers bisexual (often self-fertilizing), radially symmetrical, very small, sepals 5 (4), borne on the apex of an urceolate hypanthium (sometimes interpreted as a calyx tube with free distal lobes), petals absent; stamens 1–10, borne on the hypanthium (perigynous) just below the sepals, filaments free; ovary superior but tightly enclosed within the hypanthium, unilocular with usually 1 (2) basal ovule, styles 2, separate. Fruit a 1-seeded utricle enclosed by the hardened hypanthium and persisting sepals; seed lenticular and smooth.

A genus of perhaps 10 species native to Europe, Asia, South Africa, Australia, New Guinea, and New Zealand. The small size of the plants and crowding of flowers and axillary branches with condensed internodes produce a characteristic appearance similar to that of *Spergula arvensis*.

***Scleranthus annuus* L., Sp. Pl. 406. 1753. Figure 41.**

Herbs, annual, decumbent or ascending to 20 cm tall, much branched, leafy internodes 0–30 mm long, sparsely puberulent. Leaves sessile and clasping the leaf at their base; laminae 3–10 (20) mm long, linear or subulate, the sheathing leaf base united with the opposing leaf base to form a very short sheath, entire, glabrous on the surfaces but the basal margins ciliate, venation obscure. Inflorescence a compact few-flowered cymose cluster exceeded by the leaflike bracts, flowers subsessile; sepals 5, 1.2–2.5 mm long, lanceolate with a thick midrib, borne at the apex of the urceolate or deeply cup-shaped hypanthium, the hypanthium ca. 1.5 mm long, glabrous, with 10 indistinct ribs; stamens ca. 0.5 mm long; ovary ca. 0.9 mm long and 0.5 mm thick, styles 2, ca. 0.7 mm long, linear. Fruit enclosed within the hardened hypanthium, 3–5 mm long (including the sepals), the persisting sepals erect to slightly incurved, ca. 1–2 mm long; seeds 0.7–1 mm long, ellipsoid to ovoid, pale yellowish, with a small projection at the apex and shallow vertical depressions on each of the 2 slightly flattened faces.

Small weedy plants of open sites; collected by Brenes in June 1906 from along the Rio Reventado at 1,500 m and more recently on the slopes of Volcan Irazu at about 2,400 m, both in the province of Cartago. This species is native to north-western Europe and is now established in North America from Mexico to Canada and in the mountains of Ecuador.

*Scleranthus annuus* is recognized by its small stature, narrow little leaves expanded and united across the stems at their base, flowers and fruit in dense little clusters, and the urceolate hypanthium with five distal sepals tightly enclosing the fruit.

### SILENE Linnaeus

Herbs or small shrubs, glabrous to puberulent; stipules absent. Leaves opposite or whorled, sessile or petiolate, the sheathing bases connate or free, usually entire and

pinnately veined. Inflorescences cymes, racemes, dichasia or the flowers solitary, pedicels bracteate only at the base (an epicalyx absent). Flowers bisexual, radially symmetrical, calyx tubular with (5) 10–30 veins, ovoid to turbinate or campanulate in form, 5-toothed at the apex, petals 5, narrowed at the base to form a distinct claw and usually with appendages at the junction of claw and blade, the blade entire or more commonly lobed or toothed; stamens 10, usually borne at the apex of the androgynophore, filaments sometimes united at the base; pistil borne on the androgynophore, ovary 3-locular at the base but 1-locular above, with many ovules on a free-central placenta, styles 3 (rarely 4 or 5). Fruit a capsule dehiscent only at the apex with 6 (3, 8, 10) short teeth, borne on a carpophore, calyx persisting in fruit and slightly inflated but little enlarged and often splitting; seeds reniform to subcircular, slightly flattened on 2 faces, minutely tuberculate.

A genus of nearly 400 species, nearly all from the Old World. Both species included here are natives of Europe. They are distinguished by the lack of an epicalyx, three styles, and calyx tube with 10 or more veins.

- 1a Plants glabrous; grown in gardens for the showy flowers ..... *S. armeria*  
 1b Plants densely pubescent; weeds of higher elevations..... *S. gallica*

***Silene armeria* L., Sp. Pl. 420. 1753.**

Erect, annual, mostly glabrous herbs to 70 cm. Leaves 4–8 cm long, 1–2.5 cm wide, sessile, lanceolate to ovate, apically acute to acuminate, clasping at the base and sometimes slightly connate. Inflorescence a crowded compound dichasium, many flowered; pedicels 1–4 mm long (to 20 mm for the terminal flower), ebracteate; calyx 1.4–1.6 cm long, clavate at anthesis, becoming abruptly expanded in its distal half by the expanding stipitate fruit, 10-nerved, 5-toothed, the teeth rounded; petals 5, blades entire or emarginate, the 2 appendages ca. 2 mm long, linear, the blades pink to purple, the corolla ca. 15 mm in diameter.

This species is called *Llovizna* and *Espanola* in Central America; the English common name is "Sweet William Catchfly." The glaucous and glabrous leaves are distinctive.

***Silene gallica* L., Sp. Pl. 417. 1753. *S. anglica* L., loc. cit. 416.**

Herbs, annual, erect or spreading, 15–50 cm tall, villous-puberulent throughout and glandular-pubescent on the distal portions of the plant, leafy internodes (3) 4–9 cm long, with short scurfy to longer translucent and crooked hairs (0.3–2.5 mm). Leaves sessile or short (0–5 mm) petiolate, the lower laminae 3–5 (7) cm long, spatulate, rounded at the apex and often mucronate, tapering to the connate base, upper laminae smaller and narrower with acute apices. Inflorescence a terminal 1-sided raceme, rachis glandular-pubescent, upper pedicels very short (0.5–5 mm), pedicels subtended by a pair of linear leaflike bracts 8–20 mm long. Flowers with calyx tubes 7–10 mm long, becoming 5 mm in diameter in fruit, with 10 veins, calyx teeth ca. 2 mm long, linear, villous with crooked hairs to 3 mm long; petals bifid or toothed at the apex, entire below, white to pale purple, exceeding the calyx by ca. 1 mm, basal appendages oblong, ca. 1 mm long. Fruit a capsule 6–9 mm long, ovoid, dehiscent by 6 teeth, the teeth short (1 mm), acute, recurved; seeds ca. 1 mm broad, cochleate with rows of tubercles.

This species is a native of southern and central Europe now widely naturalized in the New World. It is a plant of open weedy sites and cultivated fields in Central America. In Costa Rica it is found between 1,600 and 2,400 m around the Meseta Central; it flowers in the wet season between April and November.

*Silene gallica* can be distinguished from our other members of the family by the viscid glandular hairs on distal parts, the one-sided inflorescence, the tubular calyx, and the capsule opening only at the apex with six small teeth.

## SPERGULA Linnaeus

Herbs, annual, usually much branched from the base, the stems decumbent to ascending, mostly glandular pubescent, rarely glabrous; stipules present and small. Leaves opposite or appearing verticillate by crowding of leafy axillary branches with condensed internodes, simple and entire, sessile or subsessile, linear or subulate. Inflorescences dichasial and terminal, small bracts present and subtending the slender pedicels; flowers bisexual, radially symmetrical, small, sepals 5, free and imbricate, petals 5, free, margins entire, white; stamens 5–10, filaments arising from a hypogynous ridge, free, anthers dehiscing longitudinally; ovary 1-locular, placentation basal with many ovules, styles 5, alternate with the sepals, free to the base. Fruit a capsule dehiscing by 5 valves, loosely enclosed within the persisting sepals, valves thin walled; seeds lenticular to subglobose, suborbicular in outline, with an acute or winged circumferential margin, surface often papillose.

A genus of four species native to Europe and Asia; one species has become widely naturalized in the New World. The verticillate appearance of leaves at most all the nodes (because of the condensed axillary shoots) is very distinctive. *Spergula arvensis* is somewhat similar in appearance and habit to *Polycarpha corymbosa* (L.) Lam. which is known to range from South America into southern Panama. However, the inflorescences of *P. corymbosa* are congested, and the cochleate seeds lack the thin winglike margin and minutely papillose surface found in *Spergula*.

***Spergula arvensis* L., Sp. Pl. 440. 1753. Figure 41.**

Erect to spreading much-branched herbs to 40 cm tall, stems and foliage glabrous below but often becoming glandular-viscid on the upper portions, internodes 1.5–6 cm long; stipules 0.8–1.5 mm long, triangular, acute to obtuse, scarious. Leaves congested at the nodes in verticillate-like clusters, sessile; laminae 1–3.5 cm long, 0.3–0.8 mm broad (dry), linear to subulate, entire, minutely puberulent with thin whitish hairs ca. 0.2 mm long. Inflorescences a compound dichasium with the terminal portions becoming racemose, to 20 cm long, lax, 10- to 30-flowered, pedicels 1–1.5 cm long, slender, usually glandular-viscid; flowers ca. 3 mm long (dry), sepals 2.5–3.5 mm long, persistent in fruit and becoming 4 mm long, ovate, acute to obtuse, usually viscid, the margins thin; petals 2–3.5 mm long, as long or slightly shorter than the sepals, entire, often persistent in fruit; stamens usually 10, 1–1.5 mm long; ovary ca. 2.5 mm long, subglobose, styles 5, ca. 0.5 mm long, curved. Fruit a capsule 3.5–5 mm long, as long as or slightly exceeding the sepals, ovoid; seeds ca. 1 mm broad and 0.7 mm thick, subglobose, with a narrow whitish circumferential ridge, the broad surfaces brown to black and usually covered with minute yellowish clavate papillae.

A native of Europe but now widely naturalized in North America and in the higher elevations of Guatemala and western Panama. Collections by Jorge Gomez-Laurito near Tierra Blanca, and by Robert Wilbur along the Carretera Interamericana, all in the province of Cartago, are the first recorded from Costa Rica. This species is a weed of open fields and also grows in sandy areas along rivers and streams, between 1,400 and 3,200 m elevation in Central America. The majority of Central American collections have been made in January and February, but the Costa Rican collections were made in June, July, and December.

## STELLARIA Linnaeus

Herbs, annual or perennial, generally with slender procumbent or clambering, repent or ascending (occasionally pendent) stems, puberulent or glabrous; stipules absent. Leaves



opposite, sessile or petiolate, often clasping the stem at their base, laminae entire, broad or narrow, venation usually pinnate and with a slender submarginal vein. Inflorescences of distal dichasial cymes subtended by reduced sessile leaves (bracts) or the flowers solitary in axils of distal leaves, a progression of basal petiolate leaves to smaller sessile distal bracts often present on flowering stems, flowers usually subtended by slender pedicels. Flowers bisexual, radially symmetrical, small, sepals 4 or 5, free to the base, imbricate, petals as many as the sepals (rarely absent), 2-cleft (bifid and often giving the appearance of 8 or 10 petals), white, lacking basal appendages; stamens 10 or fewer, free, staminodes absent; ovary superior and unilocular with basal, central or free central placentation, ovules few to many, styles 2 or 3 (rarely 4 or 5), free. Fruit a capsule, globose, ovoid, or oblong, dehiscent by as many or twice as many valves as there are styles, valves thin walled; seeds (1) few to many, cochleate to reniform or globose, usually reddish brown, the surface smooth to rugose, muricate, papillate, or tuberculate.

A genus of about 100 species, most abundant in the cooler parts of both the northern and southern temperate zones and usually at higher elevations in the tropics. These plants can be mistaken for species of *Cerastium* or *Drymaria*, but our species of *Stellaria* can be distinguished by the presence of a slender submarginal collecting vein which unites the secondary veins near the edge of the leaf and runs parallel with the margin in the distal half of the lamina (but this is not always easy to see).

- 1a Laminae lanceolate to oblanceolate, to 8 mm long, drying stiff; stems conspicuously 4-ridged, ridge continuous with the midvein of the leaf; internodes to 15 mm long; rare endemics of the eastern volcanoes; 1,600–2,600 m elevation . . . . . *S. nubigena*
- 1b Laminae lanceolate to ovate, cordate or triangular, to 5 mm long, drying thin and membranous; internodes usually becoming more than 2 cm long, rarely with 4 longitudinal ridges . . . . . 2a
- 2a Sepals and petals 4, sepals to 2.5 mm long, inflorescence a compound dichasium; stems with ridges that are continuous with midveins of the leaves; leaves often broadly cordate; 1,500–3,300 m . . . . . *S. irazuensis*
- 2b Sepals and petals 5; stems usually terete and lacking ridges extending into the midvein . . . . . 3a
- 3a Inflorescence a compound dichasium; sepals and petals 2–3.5 mm long; leaves truncate to subcordate; mostly between 600 and 2,000 m elevation . . . . . *S. prostrata*
- 3b Flowers solitary in the axils of leaves or of large leaflike bracts . . . . . 4a
- 4a Sepals 2.5–4 mm long, petals to 4.5 mm long; petioles 0–5 mm long, laminae truncate to obtuse at the base; 50–1,800 (2,300) m . . . . . *S. ovata*
- 4b Sepals 4–6 mm long, petals 7–13 mm long; petioles 4–25 mm long, laminae subcordate to cordate at the base; (1,800) 2,400–3,200 m . . . . . *S. cuspidata*

***Stellaria cuspidata*** Willd. ex Schlecht., Mag. Ges. Naturf. Freund. Berlin 7:196. 1916. *S. ciliata* Vahl ex Pers., Syn. 1:503. 1805, not Gilib., 1781. *S. limitanea* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22:74. 1940.

Herbs, annual (perhaps perennials), much branched, stems procumbent to ascending, clambering and pendent, growing over other plants to 2 m high, internodes of the main stems to 14 cm long, mostly glabrous and becoming pale yellowish, internodes of the axillary shoots mostly 1–2 cm long, often villous, 0.5–1.5 mm thick (dry). Leaves opposite, sheathing bases of opposing leaves slightly connate, petioles 4–12 (25) mm long (in ours); laminae 5–16 (22) mm long, 3–14 (18) mm wide, deltoid to narrowly triangular, acute to acuminate at the apex and with a mucronate tip, abruptly truncate to cordate at the base and the basal lobes slightly unequal, margins entire, drying membranaceous to chartaceous, villous to glabrous, secondary veins usually obscure, the submarginal vein ca. 0.3 mm from the edge. Flowers usually solitary and axillary, often with 1 or 2 flowers at distal nodes, pedicels (10) 20–40 mm long, sparsely to densely villous; sepals 5, 4–6 mm long, 1.5–2.5 mm broad, narrowly ovate to elliptic, sparsely to densely villous, the margins membranous or scarious, expanding somewhat in fruit, petals deeply bilobed for over half their length (and often appearing as 10 petals), 7–13 mm long, white; stamens 4.5–7 mm

long; ovary 2–2.5 mm long, cylindrical, styles usually 3, 2–3 mm long. Capsule 6–11 mm long, ovoid to ellipsoid; seeds ca. 1 mm broad, cochleate splitting into 3 valves, valves deeply bifid; seeds ca. 1.1 mm broad, cochleate, the tubercles rounded, reddish brown.

Plants of high montane forest formations from (1,800) 2,400 to 3,200 m elevation (to 4,000 m in Guatemala). Central American flowering and fruiting collections have been made primarily from December through March (no collections have been seen from April and May). This species, whose name and circumscription are uncertain, ranges from the southernmost United States and Mexico through Central America to Colombia and Ecuador.

*Stellaria cuspidata* is recognized by its long scrambling stems, relatively narrow, cordate to triangular, leaves, and relatively large flowers borne singly in the axils of leaves (or large leaflike bracts). The species is sometimes confused with specimens of *S. prostrata*, with usually broader leaves, smaller flowers, and from lower elevations; compare that species.

It is difficult to see why these plants were placed under the European *S. nemorum* L. Plants of *S. nemorum* have thicker erect stems usually branched only in the distal inflorescence, basal leaves twice as large and with winged petioles, and the flowers are usually borne on distal inflorescence-like stems with greatly reduced leaves (i.e., bracts). Our use of the name *S. cuspidata* is consistent with its usage in the Flora of Guatemala. However, a photo said to be type material from Ecuador looks rather different from typical Mexican and Central American material placed here. The Ecuadorean specimen has larger leaves on longer petioles, and the flowers are on long pedicels, but the sepals appear to be the same as in our material. A type photograph of *S. ciliata* Vahl and collections from northern South America placed under *S. ciliata* are very similar to our material; we follow the treatment in the Flora of Peru by considering all of these as variants of the same species.

***Stellaria irazuensis* Donnell Smith, Bot. Gaz. 23:236. 1897.**

Herbs, perennial, prostrate or spreading, usually much branched, leafy internodes 1–10 cm long, 0.4–2 mm thick, glabrous, becoming pale yellowish when dry. Leaves opposite, usually evenly spaced along the stems, petioles 6–25 mm long, sparsely villous with slender crooked translucent hairs ca. 1 mm long; laminae 10–20 (40) mm long, 7–15 (25) mm broad, deltoid to triangular or ovate, acuminate to abruptly attenuate at the apex, rounded at the truncate to cordate base, margin entire, laminae drying membranaceous and light green, sparsely villous, with 2 or 3 pairs of major secondary veins and a slender submarginal vein running parallel with the edge of the lamina ca. 0.5 mm from the margin. Inflorescences to 25 cm long, terminal or appearing to be axillary, of open dichotomously branching cymes, a pair of bracts at each dichotomy with the basal pair of bracts leaflike and sessile and the successive bracts becoming smaller, primary peduncle 4–15 cm long, each succeeding peduncle becoming shorter by  $\frac{1}{3}$ – $\frac{1}{2}$ , pedicels sparsely to densely glandular-villous. Flowers 4-parted, sepals 1.2–2.5 mm long, 0.5–1 mm broad, elliptic, acute to obtuse, glabrous; petals 4, 2–4 mm long, deeply cleft, the lobes 1.5–3.5 mm long, white; stamens 4–8, ca. 1.5 mm long, ovules 3–6 on basal placentae. Capsule ellipsoid, 1.5–2.5 mm long, subtended by the persisting sepals and petals, dehiscing by 4 valves; seeds 1–1.3 mm broad, cochleate, dark reddish brown, with a tuberculate surface.

Plants of wet evergreen montane formations between 1,500 and 2,800 m elevation (to 3,300 m in Guatemala). Flowering collections have been made primarily between June and January, with a few collections made in February and March. This species ranges from Chiapas, Mexico, to Guatemala, Nicaragua, Costa Rica, and the westernmost highlands of Panama (we have seen no collections from El Salvador or Honduras).

*Stellaria irazuensis* is distinguished by its very small four-parted flowers, the open inflorescences with long peduncles and widely spaced cymes, and the deltoid to cordate leaves that dry thin and translucent green. This species is apparently a close relative of *S. venezuelana* Steyererm.

***Stellaria nubigena*** Standley, J. Wash. Acad. Sci. 17:250. 1927.

Herbs, perennial, much branched and often forming clumps or mats, stems to 15 cm long, leafy internodes 5–15 mm long, glabrous, sharply 4-angled (in cross section), drying pale yellowish. Leaves opposite, decussate and sessile, clasping the stem at their base and the bases of opposing leaves arising close together; laminae 4–8 mm long, 1–2.5 mm wide, lanceolate to oblanceolate, apex acute and with a calloused tip, margin entire, blades thick, stiff, drying yellow to yellow-green, distally glabrous and villous near the base, midvein continuous with the ridges of the stem, secondary veins inconspicuous, submarginal veins obscure. Inflorescence few-flowered cymes or the flowers solitary, peduncles 2.5–5 mm long and subtended by a pair of scarious bracts 1.5–2 mm long, pedicels 4–10 mm long, glabrous, subtended by a pair of scarious bracts 1–1.5 mm long. Flowers 5-parted, sepals ca. 2 mm long at anthesis (up to 3 mm in fruit), lanceolate, glabrous, green with a scarious margin, petals 5, shorter than the sepals (ca. 1 mm at anthesis to 2 mm in fruit), 2-cleft nearly to the base, white; stamens apparently 8, unequal, the largest to 1 mm long; ovary ovoid, ca. 1 mm long, styles 3, 0.7–0.9 mm long. Capsule ca. 3 mm long, ovoid, splitting into 6 valves; seeds ca. 0.7 mm broad, cochleate-reniform, tuberculate, reddish brown.

*Stellaria nubigena* is endemic to Costa Rica and known only from collections by Paul Standley on Volcan Turrialba (35344, the type, US) and on the slope of Volcan Irazu near Las Nubes, San Jose (numbers 38736, 38784, and 38829) collected in February and March of 1924 between 1,600 and 2,600 m elevation. This species is easily distinguished from our other species of *Stellaria* by its stiff little sessile lanceolate leaves, short internodes, and four-angled stems.

***Stellaria ovata*** Willd. ex Schlecht., Mag. Ges. Naturf. Freund. Berlin 7:196. 1816. Figure 42.

Herbs, perennial, prostrate or spreading to 60 cm long, much branched from the base, leafy internodes 0.4–6 cm long, 0.5–1.5 mm thick, glabrous to densely hirtellous, the trichomes thin and translucent, to 1 mm long, stems green to pale yellowish when dry, and longitudinally ridged. Leaves opposite and usually evenly spaced along the stem, petioles 0–5 mm long, with lateral margins continuous with the lamina margins; laminae 5–25 (30) mm long, 7–14 mm wide, ovate to triangular, acute to obtuse at the apex and with a minute (0.7 mm) mucronate tip, attenuate at the base and decurrent on the winged petiole, drying yellowish or greenish, hirtellous, with 2–4 pairs of major secondary veins, submarginal vein 0.2–0.4 mm from the margin and often obscure. Flowers solitary in the axils of leaves, borne on long (6–25 mm) slender (0.3 mm) ebracteate hirtellous pedicels (rarely glabrous); sepals 5, 2.5–4 mm long, ovate to obovate, apically acute to obtuse, often hirtellous, petals 5, 3.5–4.5 mm long, bilobed, lobes to 1 mm long, white; stamens 10, ca. 3 mm long; ovary ovoid 2.5–3.5 mm long, with numerous ovules on a basal placenta, styles 3. Capsule 3–4 mm long, ovoid; seeds 1 mm broad, subreniform to subcircular in outline, dull reddish brown, with rows of prominent tubercles to 0.2 mm high.

Plants of moist or shaded areas in regions of evergreen vegetation formations between 50 and 1,800 (2,300) m elevation, having been collected on the Caribbean slopes and lowlands, the Central Highlands, the General Valley, and the Golfo Dulce area in Costa Rica. Flowering collections have been made throughout the year. The species ranges from Mexico southward through Central America to Venezuela and Peru.

*Stellaria ovata* is distinguished from other species of the genus by its combination of nearly sessile ovate leaves, solitary axillary flowers, and lower elevation habitat.

***Stellaria prostrata*** Baldwin, in Elliott, Bot. South Carol. & Georgia 1:518. 1821.

Herbs, annual or perennial, stems procumbent to subscandent, to 60 cm long, leafy internodes 1–7 (12) cm long, 0.5–3 mm thick, minutely puberulent to villous with trichomes to 0.5 mm long. Leaves opposite and usually evenly spaced on the stems, petioles 10–25 mm long, with lateral wings, glabrous to sparsely villous along the margins of the wing; laminae 5–30 (40) mm long, 5–20 (35) mm broad, ovate to deltoid, acute to acuminate at the apex, truncate to subcordate at the base, slightly decurrent on the petiole, drying membranaceous and pale green, glabrous or sparsely villous along the entire margins, with 2–4 pairs of major secondary veins, submarginal vein difficult to see. Inflorescences dichasial, lax, with few to many flowers, moderately to densely villous or villous-glandular with hairs 0.1–0.5 mm long, bracts subtending the inflorescence 6–20 mm long and petiolate (leaflike), each succeeding pair of bracts becoming smaller, often villous. Flowers 5-parted, sepals 2–3.5 mm long (becoming 4.5 mm long in fruit), ovate to elliptic-lanceolate, glabrous to villous-glandular, petals 5, 2–3.5 mm long, deeply lobed, the lobes 1.3–2.5 mm long, white; stamens 1.5–2 mm long; ovary ca. 1.5 mm long, styles 3 or 4, ca. 1 mm long. Capsule 4–5.5 mm long, ellipsoid to ovoid, splitting into 6 valves, the valves thin walled and strongly revolute at the tip; seeds 0.7–1 mm broad, cochleate-reniform, with rows of minute cylindrical capitate tubercles, reddish brown.

Plants of moist and shaded sites in areas of evergreen vegetation formations between 600 and 2,000 m elevation in Costa Rica (to 4,000 m elevation in Guatemala); flowering and fruiting throughout the year, but with most collections made from December through March. The species ranges from the southern United States (Texas to Georgia and Florida) through Mexico and Central America to Colombia.

*Stellaria prostrata* is very similar to *S. irazuensis* in vegetative characteristics, but it is distinguished from that species by its larger five-parted flowers and capsule valves revolute at the tip. It has been confused with certain forms of what is here called *S. cuspidata* and can be distinguished from that species by the capitate tubercles on the seeds, the sepals usually less than 4 mm long (at anthesis), the petals usually equal to the sepals in length, and the strongly revolute capsule valves. These differences appear to be consistent with ecological differences: *S. prostrata* is most commonly found between 1,200 and 1,800 m elevation (extremes of 700 to 2,000 m), while *S. cuspidata* is usually found between 2,500 and 3,200 m (extremes of 1,900 to 4,000 m) in northern Central America. (Specimens identified as *S. prostrata* by Standley and Steyermark from over 2,000 m elevation in Guatemala are sterile.) See the discussion under *S. cuspidata*.



## INDEX

The index includes all accepted names (in roman typeface), synonyms (*italics*), common English names (roman) and vernacular names (*italics*). Page numbers of illustrations are in **boldface**. Hyphenated words and multiple words are alphabetized letter by letter.

- Abanico* 162  
*Acelga* 139  
*Acetosella* 132  
*Achyranthes* 144  
   *altissima* 165  
   *aspera* 144, **146**  
   *bettzickiana* 148  
   *brasiliana* 148  
   *calea* 173  
   *costaricensis* 151  
   *indica* 145, **146**  
   *laguroides* 151  
   *lehmannii* 153  
   *megaphylla* 151  
   *panamensis* 153  
   *prostrata* 167  
   *stenophylla* 153  
   *williamsii* 154  
*Adorno de niño* 176  
*Aethanthus nodosus* 47  
*Agdestis clematoides* 203  
*Agonandra* 15, 28  
   *brasiliensis* 29  
   *macrocarpa* 15, 28  
   *obtusifolia* 29  
   *racemosa* 29  
*Agrostema coronaria* 238  
*Aguacatía* 11  
*Aizoaceae* 213, **223**, **225**, **226**  
*Algodoncillo* 174  
*Allionia* 180  
   *violaceae* 192  
*Alternanthera* 145, **149**, **152**  
   *bettzickiana* 148, **149**  
   *bettzickiana* 148  
   *brasiliana* 148  
   *caracasana* **149**, 150  
   *costaricensis* 151, **152**  
   *ficoides* 153, 156  
   *laguroides* 151, **152**  
   *lanceolata* 153  
   *lehmannii* 153  
   *Alternanthera panamensis* 153  
     *paronychoides* **149**, 153  
     *polygonoides* 154  
     *pubiflora* **152**, 154  
     *repens* 150  
     *sessilis* 155  
     *stenophylla* 153  
     *tenella* **149**, 155  
     *williamsii* 154  
*Amaranthaceae* 142–180, **146**, **149**, **152**,  
   **158**, **163**, **171**, **223**  
*Amaranthus* 156, **158**  
   *caudatus* 159  
   *cruentus* **158**, 159  
   *dubius* 157, **158**  
   *hybridus* 157, **158**  
     subsp. *cruentus* 159  
   *hypochondriaceus* 157  
   *scariosus* **158**, 159  
   *spinosus* **158**, 160  
   *tristis* 157  
   *viridis* **158**, 161  
*Amor seco* 162  
*Andripetalum suaveolens* 11  
*Anredera vesicaria* 222  
*Antidaphne* 32, **37**  
   *viscoides* 32, **37**  
*Antigonon* 100, **104**  
   *cordatum* 106  
   *grandiflorum* 101  
   *guatemalense* 101, **104**  
   *leptopus* **104**, 106  
   *macrocarpum* 101  
*Ant-plant* 137, 138  
*Apinagia* 3  
   *myriophylla* 6  
*Apodantheae* 90  
*Apodanthes* 37, 90  
   *caseariae* 37, 91  
   *flacourtiae* 91  
   *panamensis* 91  
   *tribracteata* 91

- Arenaria* **225, 226, 229**  
*alsinoides* 229  
*guatemalensis* 229  
*lanuginosa* **225, 226, 229**  
     ssp. *guatemalensis* **226, 229–231**  
*lanuginosum* ssp. *saxosa* 229, 230  
*nemorosa* 229  
*quirosii* 231  
*saxosa* 229  
*Aristolochia* 79, **80, 81, 82**  
*anguicida* **81, 82**  
*bicolor* 84  
*bilabiata* 82  
*chapmaniana* 85  
*constricta* **80, 83**  
*costaricensis* 85  
     var. *zamorensis* 85  
*gigantea* **81, 83**  
*grandiflora* **81**  
*linearifolia* 82  
*littoralis* 84  
*loriflora* 82  
*maxima* **80, 84**  
*odoratissima* **81, 84**  
*pandurata* 84  
*pilosa* **81, 85**  
*ringens* 85  
*schmidtiana* 86  
*securidata* 83  
*sylvicola* 83  
*tonduzii* **80, 85**  
*translucida* **80, 86**  
*trilobata* **81, 86**  
*veraguensis* **80, 87**  
*Aristolochiaceae* 79, **80, 81**  
  
*Baby's Breath* 238  
*Balanophoraceae* 93, **94, 95**  
*Banksia* 8  
*Basella alba* 222  
*Basellaceae* 222, **224**  
*Batchelor's button* 169  
*Bdallophyton* 90, 91, **92**  
     *americanum* 91, **92**  
     *andreuxii* 91  
     *bambusarum* 91  
     *cerantantherum* 91  
     *oxylepis* 91  
*Beets* 139  
*Bejuco de ajo* 203  
*Bellisima* 106  
*Beta* 139  
     *vulgaris* 139  
*Bilderdykia* **104, 106**  
     *aubertii* **104, 106**  
*Black Manwood* 24  
*Blandowia myriophylla* 6  
*Bledo* 156  
*Boerhavia* 181  
     *Boerhavia coccinea* **183, 187**  
         *diffusa* 183, 188  
         *erecta* **183, 188**  
         *paniculata* 188  
*Bogambilla* 189  
*Boldoa* 199  
     *ovatifolia* 199  
     *purpurascens* 199  
*Boria* 162  
*Bougainvillea* **182, 189**  
     *buttiana* 189  
     *glabra* 190  
     *spectabilis* 189  
*Boussingaultia* 222, **224**  
     *ramosa* 222, **224**  
*Brandesia lanceolata* 153  
     *pubiflora* 154  
*Bugambilla* 189  
*Buguenvitia* 189  
  
*Calandrina megarhiza* 218  
*Caldasia cayennensis* 97  
*Calalu* 206  
*Callite* 138  
*Campderia floribunda* 120  
     *mexicana* 120  
*Camron* 176  
*Canilla de Mula* 138  
*Caraxeron* 177  
     *vermicularis* 177  
*Carnation* 234  
*Caryophyllaceae* **225, 226, 227**  
*Caryophyllales* (families 63–70) 138–247  
*Casearia* 91  
*Celosia* 161, **163**  
     *argenta* 162, **163**  
         var. *cristate* 162  
     *paniculata* 165, 175  
     *pleiogyna* 178  
     *virgata* 162, **163**  
*Centrospermae* (families 63–70) 138–247  
*Centrostachys aspera* 144  
     *indica* 145  
*Cephalotomandra* 180  
     *fragrans* 180  
     *panamensis* 180  
*Cerastium* **226, 231**  
     *caespitosum* 233  
     *fontanum* ssp. *trivale* 233  
     *glomeratum* 232  
     *guatemalense* **226, 232**  
     *holosteoides* 233  
     *trivale* 233  
     *viscosum* 232  
     *vulgatum* 233  
*Chamissoa* **163, 164**  
     *acuminata* 165  
     *altissima* **163, 165**  
     *macrocarpa* 165

- Chard 139  
 Chaunochiton 16, **18**  
   kappleri 16, **18**  
 Chenopodiaceae 138, **202**  
 Chenopodiales (families 63–70) 138–247  
 Chenopodium 140, **202**  
   album 140  
   ambrosioides 141, **202**  
   anthelminticum 141  
   quinoa 140  
*Chile de perro* 129  
*Chivito* 174  
*Chivo* 174  
 Cladocolea **35**, 38  
   oligantha **35**, 39  
*Clavel* 234  
*Clavel Imperial* 234  
*Clavellina* 235  
*Clavellina montes* 215  
*Claytonia paniculata* 221  
 Coccoloba 107, **108**, **109**, **110**, **111**  
   acapulcensis **109**, 113  
   acuminata **110**, 114  
   allenii 116  
   belizensis **111**, 114  
   browniana 113  
   caracasana **108**, 115  
   cardiophylla 113  
   changuinolana 116  
   floribunda 120  
   guanacastensis **111**, 116  
   hirsuta 114  
   lehmannii **110**, 116  
   molinae 120  
   obovata **109**, 117  
   padiformis **111**, 119  
   riparia 117  
   roseiflora 118  
   standleyana 115  
   tuerckheimii **109**, 118–119  
   uvifera **108**, 119  
   venosa **110**, 120  
   wercklei 113  
   williamsii 116  
*Colacion* 106  
*Colchón de niño* 148  
*Comentero* 174  
 Commicarpus 180  
*Confite* 106  
*Confitillo* 106  
 Conopholis 93  
*Coqueta* 148  
*Cordia alliodora* 75  
*Corynaea* **95**, 96  
   crassa **95**, 96  
   sphaerica **95**, 97  
 Cottage Pinks 235  
*Coyuntura* 174  
*Coyuntura de pollos* 176  
*Cresta de gallo* 162  
*Cricamola* 24  
*Crillo* 24  
*Cyathula* **146**, 166  
   achyranthoides **146**, 166  
   prostrata **146**, 167  
*Cynomorium cayennense* 97  
 Cytineae 90  
*Cytinus americanum* 91  
  
*Danto hediondo* 13  
*Dendrophthora* 60, **61**  
   ambigua **61**, 64  
   biserrula 65  
   costaricensis **61**, 64  
     subsp. *poasensis* 64  
   geniculata 65  
   squamigera **61**, 65  
   terminalis **61**, 66  
*Desmochaeta achyranthoides* 166  
*Dianthus* 233  
   barbatus 234  
   caryophyllus 234  
   chinensis 234  
   plumarius 235  
 Dioscorea 82  
   calyculata 222  
 Drymaria **226**, 235  
   cordata **226**, 236  
   diandra 236  
   hirsuta 237  
   multiflora 236  
   villosa 237  
     ssp. *villosa* 237  
*Dufourea hypnoides* 7  
   trifaria 7  
  
 Eremolepidaceae 31, **37**  
 Eriogonum 99  
*Escambron* 124  
*Escambron negro* 124  
*Española* 242  
*Españolita* 238  
*Espinaca* 141, 142, 213  
*Eubrachion* 31  
  
*Fallopia aubertii* 107  
*Flor de corona* 174  
*Flor de mano* 162  
*Flor de San Miguel* 106  
*Flor de Verano* 189  
*Flores de palo* 50  
 Flowering stones 213  
 Four-o'clock 192  
  
 Gaiadendron **34**, 39  
   *poasense* 39  
   punctatum **34**, 39  
*Gateador* 121

- Gipsofilia* 238  
*Glinus* 213, **226**  
     *radiatus* 214, **226**  
*Golondrina* 154  
*Gomphrena* 168  
     *brasiliensis* 148  
     *decumbens* 169  
     *dispersa* 169  
     *elegans* 168  
     *ficoidea* 153  
     *filaginoides* 168  
     *globosa* 168  
     *latifolia* 173  
     *paniculata* var. *hookeriana* 176  
     *serrata* **149**, 169  
     *sessile* 155  
     *tuerckheimii* 168  
     *vermicularis* 177  
 Grain amaranths 156, 157–159  
*Grevillea* 9, **10**  
     *banksii* 9  
     *robusta* 9, **10**  
*Guapira* **184**, 190  
     *costaricana* **184**, 190  
     *linearibracteata* 190  
     *standleyanum* 190  
*Gypsophila* 237  
     *elegans* 238  
     *paniculata* 238  
  
*Hebanthe hookerianus* 176  
*Heisteria* 17, **18**  
     *acuminata* **18**, 19, 20  
     *acuta* 23  
     *coccinea* 20  
     *concinna* **18**, 20  
     *costaricensis* **18**, 20  
     *cyanocarpa* **18**, 21  
     *eurycarpa* 22  
     *fatoensis* 22  
     *kappelerii* 16  
     *latifolia* 22  
     *longipes* 21  
     *macrophylla* **18**, 22  
     *scandens* **18**, 22  
*Helosis* **94**, **95**, 97  
     *cayennensis* **94**, **95**, 97, 98  
         var. *cayennensis* 98  
         var. *mexicana* 97, 98  
     *guyanensis* 97  
     *mexicana* 97, 98  
*Hierba de gato* 176  
*Hillieria* 203  
     *subcordata* 203  
*Holosteum cordatum* 236  
     *diandrum* 236  
*Homalocladium platycladum* 121  
*Hongo* 98  
*Hormigo* 138  
*Howardia costaricensis* 85  
     *hoffmanni* 84  
  
*Hydnora* 87  
 Hydnoraceae 87, **88**  
  
*Immortal* 169  
 Insect-plant mutualism 138  
*Iresine* 170, **171**  
     *acicularis* 176  
     *angustifolia* **171**, 172  
     *argenta* 173  
     *arrecta* **171**, 172  
     *calea* **171**, 173  
     *celosia* 175  
     *celosoides* 175  
     *costaricensis* **171**, 174  
     *diffusa* **171**, 175  
     *elatior* 172  
     *frutescens* 176  
     *grandiflora* 176  
     *hassleriana* 175  
     *latifolia* 173  
     *paniculata* 175  
     *spiculigera* 176  
  
*Jabonillo* 206  
*Jamesbondia costaricensis* 151  
  
*Lacis schiedeanum* 6  
     *foeniculacea* 4  
*Langsdorffia* **94**, 98  
     *hypogaea* **94**, 99  
*Lechugon* 134  
*Lengua de caballo* 134  
*Lengua de vaca* 134  
*Lewisia* 218  
     *megarrhiza* 218  
*Llovizna* 238, 242  
*Lora malodora* 13  
 Loranaceae (sensu lato) 29, 30, 33,  
     **34–37**, 57–63  
 Loranaceae (sensu stricto) 33, **34–37**  
*Loranthus aduncus* 45  
     *alveolatus* 41  
     *amplexicaulis* 41  
     *angustifolius* 69  
     *calyculatus* 47  
     *cansjeraefolius* 56  
     *chordocladus* 55  
     *leptostachyus* 52  
     *marginatus* 53  
     *nodosus* 47  
     *occidentalis* 42  
     *oerstedii* 54  
     *orbicularis* 55  
     *paniculatus* 45  
     *piperoides* 75  
     *punctatus* 39  
     *pyrifolius* 44  
     *quadrangularis* 75  
     *quercicola* 56



- Loranthus ramiflorus* 48  
     *retroflexus* 45  
     *schiedeanus* 49  
     *spicatus* 43  
     *theobromae* 45  
*Lustrosa* 189  
*Lychnis* 238  
     *coronaria* 238
- Mangillo* 17  
*Mano de león* 162  
*Manto de Jesús* 189  
*Manu* 24  
*Marathrum* 2, 3  
     *allenii* 5  
     *cheiriferum* 4, 5  
     *flexuosum* 6  
     *foeniculaceum* 4  
     *indifferens* 5  
     *leptophyllum* 5  
     *minutiflorum* 5  
         *forma allenii* 5  
         *forma diversifolium* 5  
         *forma indifferens* 5  
         *forma intermedium* 5  
     *oxycarpum* 5  
     *pusillum* 5  
     *schiedeanum* 2, 6  
     *tenue* 2, 6  
     *utile* 2, 7  
*Maravilla* 192  
 Medicinal uses 82, 134, 140–141  
*Melanocarpum sprucei* 179  
*Mesembryanthemum* 213  
*Microtea* 200, 204  
     *debilis* 200, 204  
*Minquartia* 15, 23  
     *guianensis* 15, 23  
*Mirabilis* 182, 191  
     *jalapa* 182, 192  
     *violaceae* 182, 192  
*Mitrastemma* 93  
*Mitrastemon* 90, 93  
     *matudai* 93  
*Mitrostemonaceae* 93  
*Mollugo* 214, 225  
     *radiata* 214  
     *tetraphylla* 239  
     *verticellata* 215, 225  
*Moño* 162  
*Moño de reina* 162  
*Monte negro* 148  
*Mosotillo* 145  
*Mozote* 145  
*Muehlenbeckia* 104, 121  
     *platyclada* 121  
     *tamnifolia* 104, 122  
     *volcanica* 123  
*Mulato* 138
- Napoleón* 189  
*Neea* 185, 186, 193  
     *acuminatissima* 195  
     *amplifolia* 186, 194, 195  
     *belizensis* 195  
     *delicatula* 185, 196  
     *elegans* 186, 194, 195  
     *latevirens* 185, 195, 196  
     *orosiana* 194  
     *pittieri* 186, 195  
     *popenoei* 185, 195, 196  
     *psychotrioides* 185, 195, 196  
     *pycnantha* 195  
     *urophylla* 194  
     *xanthina* 195  
*Negro* 24  
*Neolacis myriophylla* 6  
 New Zealand Spinach 213  
*Nispero* 24  
*Notanthera* 29  
*Nyctaginaceae* 180, 182–186
- Olacaceae* 14, 15, 18  
*Opiliaceae* 15, 27  
*Oreobroma megarhiza* 218  
     *mexicanum* 218  
*Oryctanthus* 33, 37, 40, 41  
     *alreolatus* 37, 41  
     *botryostachys* 41  
     *cordifolius* 37, 42  
     *florulentus* 43  
     *guatemalensis* 43  
     *occidentalis* 37, 42  
     *spicatus* 37, 43  
*Oxybaphus* 191  
     *violaceus* 192
- Palo de papa* 11  
*Panopsis* 9, 10  
     *costaricensis* 11  
     *suaveolens* 10, 11  
*Papa* 11  
*Papaturro* 112, 120, 121  
*Papaturro Blanco* 116  
*Papaturro de Playa* 121  
*Papaturro Negro Macho* 121  
*Papaturro Rastero* 121  
*Pasacarne* 3  
*Perico* 148  
*Peristethium leptostachyum* 52  
*Petiveria* 202, 205  
     *alliacea* 202, 205  
*Pfaffia* 152, 176  
     *grandiflora* 152, 176  
     *hookeriana* 176  
         *forma glabriuscula* 176  
*Philoxerus* 177  
     *vermicularis* 177

- Phoradendron* **61, 62, 63, 66, 67**  
*acinacifolium* **63, 68**  
*allenii* **64**  
*angustifolium* **69**  
*annulatum* **62, 69**  
*auriculatum* **72**  
*biolleyi* **75**  
*ceibanum* **75**  
*conzattii* **70**  
*cooperi* **77**  
*corynarthron* **61, 70, 76**  
     *var. seibertii* **75**  
*crassifolium* **63, 71**  
     *var. pittieri* **71**  
*crispum* **64**  
*davidsoniae* **70**  
*dichotomum* **62, 71**  
*dipterum* **62, 72**  
*dodgei* **76, 77**  
*ensifolium* **69**  
*falcifolium* **76**  
*flavens* **63, 73**  
*flavescens* **64**  
*gracilispicum* **78**  
*herrerense* **75**  
*mucronatum* **73**  
*novae-helvetiae* **77**  
*obliquum* **63, 74, 77**  
*paquitatum* **75**  
*pergranulatum* **76**  
*piperoides* **63, 75**  
*quadrangulare* **61, 75**  
*quinquenervium* **73**  
*rensonii* **75**  
*robaloense* **68**  
*robustissimum* **63, 76**  
*seibertii* **75**  
*sonarum* **75**  
*sp. aff. undulatum* **62**  
*squamigerum* **65**  
*supravenulosum* **73**  
*tonduzii* **62, 77**  
*undulatum* **62, 78**  
*venezuelense* **75**  
*woodsonii* **73**
- Phrygilanthus* **33**  
*panamensis* **55**
- Phthirusa* **33, 35, 44**  
*adunca* **45**  
*paniculata* **45**  
*pittieri* **52**  
*pyrifolia* **35, 44**  
*retroflexa* **35, 45**
- Phytolacca* **201, 206**  
*costaricensis* **208**  
*icosandra* **201, 207**  
*meziana* **206**  
*octandra* **206**  
*purpurascens* **206**  
*rivinoidea* **201, 206, 207**  
*rugosa* **201, 208**
- Phytolaccaceae* **199, 200–202, 203**
- Pilostyles* **90, 93**  
*covillei* **93**  
*globosa* **93**  
*thurberi* **93**
- Pisonia* **184, 196**  
*aculeata* **184, 197**  
     *var. macranthocarpa* **197**  
*fasciculata* **197**  
*grandifolia* **197**  
*macranthocarpa* **197**  
*sylvatica* **184, 198**
- Pleuropetalum* **163, 178**  
*calospermum* **179**  
*costaricensis* **179**  
*pleiogynum* **163, 178**  
*sprucei* **163, 179**  
*standleyi* **178**  
*tucurriquense* **179**
- Podopterus* **105, 123**  
*mexicanus* **105, 123**
- Podostemaceae* **1**
- Polycarpha corymbosa* **243**
- Polycarpon* **238**  
*tetraphyllum* **239**
- Polygonaceae* **99, 102–105, 108–111**
- Polygonum* **102, 124**  
*acuminatum* **102, 125**  
*aubertii* **106, 107**  
*aviculare* **126**  
*baldschuanicum* **106**  
*grandiflorum* **101**  
*guatemalense* **125**  
*hispidum* **102, 126**  
*hydropiper* **129**  
*hydropiperoides* **102, 127**  
*meisnerianum* **102, 128**  
*mexicanum* **129**  
*pennsylvanicum* **130**  
*persicaria* **128**  
*persicarioides* **128**  
*platycladum* **121**  
*punctatum* **102, 128, 129**  
*segetum* **102, 129**  
*tamniifolium* **122**  
*uvifera* **119**  
*volcanicum* **123**
- Pomonece* **189**
- Pompiella* **189**
- Portulaca* **218, 225**  
*coronata* **220**  
*denudata* **220**  
*grandiflora* **219**  
*lanceolata* **220**  
*marginata* **219**  
*oleracea* **219, 223**  
*paniculata* **221**  
*patens* **221**  
*pilosa* **220, 225**  
*plano-operculata* **220**  
*portulacastrum* **215**

*Portulaca umbraticola* 220  
 Portulacaceae 217, 223–225  
*Primavera* 189  
*Prosopanche* 87, 88  
   *americana* 89  
   *costaricensis* 88, 89  
*Protea* 8  
 Proteaceae 8  
*Psittacanthus* 34, 46  
   *allenii* 48  
   *calyculatus* 34, 47  
   *chrismarii* 47  
   *dilatatus* 48, 49  
   *lateriflorus* 48  
   *mayanus* 47  
   *nodosus* 34, 47  
   *ramiflorus* 34, 48  
   *scheryi* 34, 48  
   *schiedeanus* 34, 49  
*Purselane* 220

*Rabo de Chanco* 145  
*Rabo de gato* 162  
 Rafflesiaceae 89, 90, 92  
 Rainbow Pinks 235  
*Remolacha* 139  
*Rhaptostylum acuminatum* 19  
*Rheum* 130  
   *rhabarbarum* 130  
   *rhaponticum* 130  
*Rhubarb* 130  
 Ribbon Bush 122  
*Rivina* 200, 208  
   *humilis* 200, 209  
   *octandra* 211  
   *polyandra* 212  
*Rosas de palo* 50  
 Rose Champion 238  
*Roupala* 10, 11  
   *borealis* 13  
   *complicata* 13  
   *glaberrima* 10, 12  
   *loranthoides* 10, 13  
   *montana* 10, 13  
     *var. dentata* 14  
   *panamensis* 13  
*Ruibarbillo* 132  
*Ruibarbo* 130  
*Rumex* 103, 131  
   *acetosella* 103, 132  
   *costaricensis* 103, 132  
   *crispus* 103, 133  
   *peruanus* 133  
   *tolimensis* 133  
*Ruprechtia* 105, 134–135  
   *costata* 105, 135  
   *cumingii* 136  
   *deamii* 135  
   *kellermanii* 135  
   *nepalensis* 103, 134

*Ruprechtia obtusifolius* 103, 134  
   *pringlei* 136

*Sagina* 225, 239  
   *procumbens* 225, 240  
*Salpianthus* 183, 198  
   *purpurascens* 183, 199  
*San Andres* 106  
*San Diego* 169  
*San Miguel* 106  
 Santalaceae 14  
 Santalales (families 56–58) 14–79  
*Santa Rita* 189  
*Saponaria* 240  
   *officinalis* 240  
*Schoepfia* 15, 24  
   *americana* 25  
   *arborescens* 25  
   *obliquifolia* 26  
   *schreberi* 15, 25  
   *species A* 15, 26  
   *vacciniiflora* 15, 25  
*Scleranthus* 225, 241  
   *annuus* 225, 241  
 Sea Grape 120  
*Sempre Lustrosa* 189  
*Sesuvium* 215, 223  
   *portulacastrum* 215, 223  
   *scandens* 210  
*Siempreviva* 169  
*Siete pellejos* 174, 176  
*Silene* 241  
   *anglica* 242  
   *armeria* 242  
   *gallica* 242  
 Soapwort 241  
*Solitaria* 122  
*Spergula* 225, 243  
   *arvensis* 225, 243  
*Spergulastrum lanuginosum* 229  
 Spinacea oleracea 142  
 Spinach 141, 142  
 Spinach-like vegetables 217, 220–222  
*Spinacia* 141  
*Stegnosperma* 202, 210  
   *cubense* 202, 210  
   *scandens* 210  
*Stellaria* 226, 243  
   *ciliata* 244, 245  
   *cuspidata* 245  
   *irazuensis* 245  
   *limitanea* 244  
   *nemorum* 245  
   *nubigena* 246  
   *ovata* 226, 246  
   *prostrata* 247  
   *venezuelana* 246  
*Struthanthus* 35, 36, 50  
   *aff. dichotrianthus* 57  
   *belizensis* 55

*Struthanthus cansjeraefolius* 56  
*chordocladus* 55  
*costaricensis* 36, 52  
*guatemalensis* 43  
*leptostachyus* 35, 42  
*macrostachyus* 58  
*marginatus* 36, 53, 57  
*oerstedii* 36, 54  
*oliganthus* 39  
*orbicularis* 36, 55  
*panamensis* 33, 35, 55  
*papillosus* 57  
*polystachyus* 52  
*quercicola* 36, 56, 57  
*retroflexus* 45  
*rotundatus* 36, 57  
*woodsonii* 35, 58  
Sweet William 234  
Sweet William Catchfly 242

*Tabaco* 138  
*Tabaco de Monte* 138  
*Tabacon* 127, 138  
*Taba de gueguecho* 176  
*Tacuquelite* 174  
*Talinum* 221, 224  
    *paniculatum* 221, 224  
    *patens* 221  
    *triangulare* 221, 222  
*Tandonia ramosa* 222  
Tapeworm Plant 122  
*Telanthra bettzichiana* 148  
*Tenia* 122  
*Terciopelo* 162  
*Tetragonia expansa* 213  
*Thonningia* 98  
*Tinta* 206  
*Tobaquillo* 127  
*Torrubia* 190  
    *costaricana* 190  
*Tres Marias* 189  
*Trianthema* 216, 223  
    *portulacastrum* 216, 223

*Trichilia scandens* 210  
*Trichostigma* 200, 211  
    *octandrum* 200, 211  
    *polyandrum* 200, 211  
*Trinitaria* 189  
*Triplaris* 108, 136  
    *cumingiana* 137, 138  
    *macombii* 137  
    *melaenodendron* 105, 137  
*Tristicha* 2, 7  
    *hypnoides* 7  
*Tsu-Kra* 27  
*Turi-Svan-Kra* 138

*Ullucus tuberosa* 222  
*Uña de Tigre* 198  
*Uva* 120  
*Uva de Playa* 120

Vegetables 134, 141, 142, 156, 217, 220, 221  
*Velasquezia melaenodendron* 137  
*Velo de gueguecho* 176  
*Velo de princesa* 176  
*Veranera* 189  
*Verdolaga* 217, 220, 221  
Viscaceae 57–63  
*Viscum angustifolium* 69  
    *cordifolium* 42  
    *crassifolium* 71  
    *dichotomum* 71  
    *ensifolium* 69  
    *flavens* 73  
    *mucronatum* 73  
    *squamigerum* 65  
*Vomita* 203

Ximenez, Francisco 27  
*Ximania* 15, 26  
    *americana* 15, 27





Families of seed plants known or expected to occur in Costa Rica and adjacent areas numbered according to the sequence of Engler's *Syllabus der Pflanzenfamilien*, edition 11, reworked by L. Diels (1936).

1	Cycadaceae	78	Myristicaceae	153	Begoniaceae
2	Taxaceae	79	Monimiaceae	154	Cactaceae
3	Podocarpaceae	80	Lauraceae	155	Thymelaeaceae
4	Araucariaceae	81	Hernandiaceae	156	Elaeagnaceae
5	Pinaceae	82	Papaveraceae	157	Lythraceae
6	Cupressaceae		incl. Fumariaceae	158	Punicaceae
7	Gnetaceae	83	Capparidaceae	159	Lecythidaceae
8	Typhaceae	84	Cruciferae	160	Rhizophoraceae
9	Potamogetonaceae	85	Tovariaceae	161	Combretaceae
10	Najadaceae	86	Resedaceae	162	Myrtaceae
11	Alismataceae	87	Moringaceae	163	Melastomataceae
12	Butomaceae	88	Droseraceae	164	Onagraceae
13	Hydrocharitaceae	89	Crassulaceae	165	Halorrhagaceae
14	Truridaceae	90	Saxifragaceae	166	Araliaceae
15	Gramineae	91	Brunelliaceae	167	Umbelliferae
16	Cyperaceae	92	Cunoniaceae	168	Cornaceae
17	Palmae	93	Hamamelidaceae	169	Clethraceae
18	Cyclanthaceae	94	Rosaceae	170	Monotropaceae
19	Araceae	95	Connaraceae	171	Pyrolaceae
20	Lemnaceae	96	Leguminosae	172	Ericaceae
21	Mayacaceae	97	Krameriaceae	173	Theophrastaceae
22	Xyridaceae	98	Oxalidaceae	174	Myrsinaceae
23	Eriocaulaceae	99	Geraniaceae	175	Primulaceae
24	Bromeliaceae	100	Tropaeolaceae	176	Plumbaginaceae
25	Commelinaceae	101	Linaceae	177	Sapotaceae
26	Pontederiaceae		incl. Humiriaceae	178	Ebenaceae
27	Juncaceae	102	Erythroxylaceae	179	Symplocaceae
28	Liliaceae	103	Zygophyllaceae	180	Styracaceae
29	Haemodoraceae	104	Rutaceae	181	Oleaceae
30	Amaryllidaceae	105	Simarubaceae	182	Loganiaceae
31	Velloziaceae	106	Burseraceae	183	Gentianaceae
32	Dioscoreaceae	107	Meliaceae	184	Apocynaceae
33	Iridaceae	108	Malpighiaceae	185	Asclepiadaceae
34	Musaceae	109	Trigonaceae	186	Convolvulaceae
35	Zingiberaceae	110	Vochysiaceae	187	Polemoniaceae
36	Cannaceae	111	Polygalaceae	188	Hydrophyllaceae
37	Marantaceae	112	Dichapetalaceae	189	Boraginaceae
38	Burmanniaceae	113	Euphorbiaceae	190	Verbenaceae
39	Orchidaceae	114	Callitrichaceae	191	Labiatae
40	Casuarinaceae	115	Buxaceae	192	Solanaceae
41	Piperaceae	116	Coriariaceae	193	Scrophulariaceae
42	Chloranthaceae	117	Anacardiaceae	194	Bignoniaceae
43	Lacistemaeae	118	Cyrtellaceae	195	Pedaliaceae
44	Salicaceae	119	Aquifoliaceae	196	Martyniaceae
45	Garryaceae	120	Celastraceae	197	Orobanchaceae
46	Myricaceae	121	Hippocrateaceae	198	Gesneriaceae
47	Juglandaceae	122	Staphyleaceae	199	Lentibulariaceae
48	Batidaceae	123	Icacinaceae	200	Acanthaceae
49	Betulaceae	124	Hippocastanaceae	201	Plantaginaceae
50	Fagaceae	125	Sapindaceae	202	Rubiaceae
51	Ulmaceae	126	Sabiaceae	203	Caprifoliaceae
52	Moraceae	127	Balsaminaceae	204	Valerianaceae
53	Urticaceae	128	Rhamnaceae	205	Dipsacaceae
54	Podostemonaceae	129	Vitaceae	206	Cucurbitaceae
55	Proteaceae	130	Elaeocarpaceae	207	Campanulaceae
56	Olaceae	131	Tiliaceae	208	Compositae
57	Opiliaceae	132	Malvaceae		
58	Loranthaceae	133	Bombacaceae		
59	Aristolochiaceae	134	Sterculiaceae		
60a	Hydnoraceae	135	Dilleniaceae		
60b	Rafflesiaceae	136	Actinidiaceae		
61	Balanophoraceae	137	Ochnaceae		
62	Polygonaceae	138	Caryocaraceae		
63	Chenopodiaceae	139	Marcgraviaceae		
64	Amaranthaceae	140	Quinaceae		
65	Nyctaginaceae	141	Theaceae		
66	Phytolaccaceae	142	Guttiferae		
67	Aizoaceae		incl. Hypericaceae		
68	Portulacaceae	143	Elatinaceae		
69	Basellaceae	144	Cistaceae		
70	Caryophyllaceae	145	Bixaceae		
71	Nymphaeaceae	146	Cochlospermaceae		
72	Ceratophyllaceae	147	Violaceae		
73	Ranunculaceae	148	Flacourtiaceae		
74	Berberidaceae	149	Turneraceae		
75	Menispermaceae	150	Passifloraceae		
76	Magnoliaceae	151	Caricaceae		
77	Anonaceae	152	Loasaceae		

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